The

American Midland Naturalist

Founded by J. A. Nieuwland, C.S.C.

●

CONTENTS

Vol. 63 APRIL, 1960 No. 2

The AMERICAN MIDLAND NATURALIST is a general biological periodical published quarterly by the University of Notre Dame. It welcomes to its pages articles of a descriptive, analytical, and experimental nature. Review articles on topics of current interest in the various fields of Biology are also welcome.

Subscription rate per year $10.00 in the U. S., Mexico, and South American countries; $11.00 elsewhere.

Address All Correspondence to:

AMERICAN MIDLAND NATURALIST
University of Notre Dame
Notre Dame, Indiana

Entered as second-class matter at Notre Dame, Indiana. Accepted for mailing at special rate of postage provided for in section 1103; Act of October 3, 1917, authorized on July 3, 1918.

The American Midland Naturalist

Published Quarterly by The University of Notre Dame, Notre Dame, Indiana

Vol. 63 APRIL, 1960 No. 2

Studies Concerning the Effects of Nutrition on Morphology of Amebas. I. Mayorella cultura Bovee, on Abundant and Starvation Quantities*

EUGENE C. BOVEE

University of Florida, Gainesville

Students of the morphology and taxonomy of the naked, lobose amebas of the order Amoebida (Hall, 1953) have long been aware that various ecological conditions might be construed to cause morphological variations such that classical methods of taxonomic discrimination [i.e. use of pseudopods (Schaeffer, 1916, 1926) which are dependent on locomotive activities] may not always be wholly reliable (Bovee, 1953; Jepps, 1956; Leidy, 1879; Mast, 1928; Penard, 1902; Schaeffer, *loc. cit.*).

Thus some researchers have attempted to dismiss from consideration all ameboid morphologies other than those of the nuclei or the mitotic variations thereof, deeming mainly the nuclei to be of taxonomic value (Calkins, 1907; 1913, 1926; Hyman, 1940; Jepps, *loc. cit.;* Kudo, 1952, 1954, 1959; Minchin, 1911; Reichenow, 1953; Singh, 1952; Wenyon, 1926).

Physiological tests of some stringency beyond normally encountered limits have produced results (Brinley, 1928; Daugherty, 1937; Edwards, 1924; Hopkins, 1928; Jennings, 1906; Kriszat, 1952; Mast, 1928, 1929; Morita and Chambers, 1929; Nardone, *et al.*, 1956; Neresheimer, 1905; Pantin, 1926; Ray and Hayes, 1954; Reznikoff and Chambers, 1927; Seifriz, 1939; Verworn, 1903) which sometimes are quoted (or occasionally misquoted) by critics of locomotive taxonomic criteria in support of their complaints, thus further confusing the problem.

Despite the criticisms from all such sources, little has been done to find whether and to what extent, ecological variations normally encountered by amebas might affect locomotive morphologies and therefore their taxonomic utility.

We[1] have been able to grow clonal cultures of a small ameba of

---

* Supported by NIH Research Grant E-1158, and the University of Florida.

[1] I wish to express my thanks to Mrs. Jacqueline Hynes, who, as my research associate, developed the techniques of clonal and axenic cultures herein described; and who brought to my attention the apparent effects of starvation on these amebas.

stagnant freshwaters, *Mayorella cultura* (Bovee, 1960) which forms locomotive pseudopods of the clear, conical, determinate shape characteristic of the family *Mayorellidae* Schaeffer 1926. These we have tested on abundant and on starvation quantities of food, and have observed the effects on its locomotive morphologies.

Materials and Methods

The ameba was found in a water sample collected June 26, 1957, at the shaded south shore of a small lake ("Bivin's Arm") at the southern periphery of Gainesville, Florida. There was much aquatic vegetation (*Elodea, Potomogeton, Lemna*) and vegetable detritus at the site. The water temperature was 27° C.; pH was about 6.5.

At the time the ameba was first seen on July 24, 1957, the temperature of the water sample was 22° C., and pH again somewhat acid, at 6.4.

The microscope slide bearing the water droplet and the cover slip were placed separately, wet side down, upon sterile, nutrient Cerophyll-agar (Bovee, 1959a) in a covered Petri dish, and incubated at 22° C. for five days. Amebas then feeding on native bacteria were numerous, as were the bacteria. Transfers were made thereafter at 10 to 12 day intervals, and an overlay of aqueous saline (Neff, 1957) added. The cultures were flourishing by mid-December 1957.

On January 31, 1958, clonal cultures were established by transfer of individual cysts to non-nutrient agar plates to which 0.2 ml. of antibiotic mix had been added to inhibit bacterial growth (200 mg. penicillin and 200 mg. streptomycin in 10 cc. of distilled water).

From one of these clones during February 2 to 5, 1958, other clones were established on four other agar plates: (1) nutrient cerophyll agar; (2) nutrient cerophyll agar with liquid overlay of 5 cc. of Neff's ameba saline; (3) non-nutrient agar; and (4) non-nutrient agar with liquid overlay. All four types of cultures were also established with the antibiotic mix *addendum* which restricted the bacterial rate of increase to a low order, but did not appear to affect the amebas.

Observations were made over a period of about two weeks, until practically all the trophic amebas had encysted, then excysted, and once more encysted.

A Bausch and Lomb phase contrast microscope was used at 200× for observation of the mayorellas on the agar plates. An American Optical-Baker interferometer microscope with shearing-focus condensors and objectives at 100× and 400 × was used for detailed observations of morphology; the amebas were studied after transference to a drop of Neff's ameba saline on a clean glass slide, and covered with a clean cover slip.

Light was provided by a Bausch and Lomb research-type microscope lamp model 31-26-33, with or without ground-glass, "daylight blue," sodium-green, and heat-filtering glass filters, singly or in various combinations.

Measurements of amebas were made at 200× with the phase contrast, and at 400× with the interferometer system, by means of a calibrated ocular micrometer.

The pH was controlled within narrow limits by the employment of Neff's buffered ameba saline both in the liquid component of the agar, and as the liquid overlay where used. The pH of the agar thus prepared was 6.4, and that of the saline, 6.5. Oxygen was continually available to the amebas since the petri dishes were kept covered but not sealed.

Inoculations and transfers were made by standard, sterile bacteriological techniques with a wire loop of nichrome alloy. Media were prepared by standard bacteriological methods. Individual cysts were picked out with sterile glass micropipettes and transferred.

RESULTS AND OBSERVATIONS

Both bacteria and amebas grew abundantly and continuously during the observation period on the cerophyll-agar either with or without overlay. The antibiotic mix somewhat slowed bacterial growth when added to the cerophyll media, but there was always enough bacterial food for the amebas. The cerophyll extract, proteose-peptone, glucose and salts in the agar provided an abundant nutritive *quantum* for the bacteria.

On the non-nutrient agar, which contained only added salts and water, even with the overlay, bacterial growth was very slow; and was even slower on that which contained the antibiotics. On the latter, after four days, only a few amebas were present. These remained upon or at the periphery of the few small colonies of bacteria, feeding upon them. A few amebas and bacteria were present until about seven days after clonal establishment. In eight or nine days only an occasional trophic ameba was found, a few encysted amebas and very few bacteria.

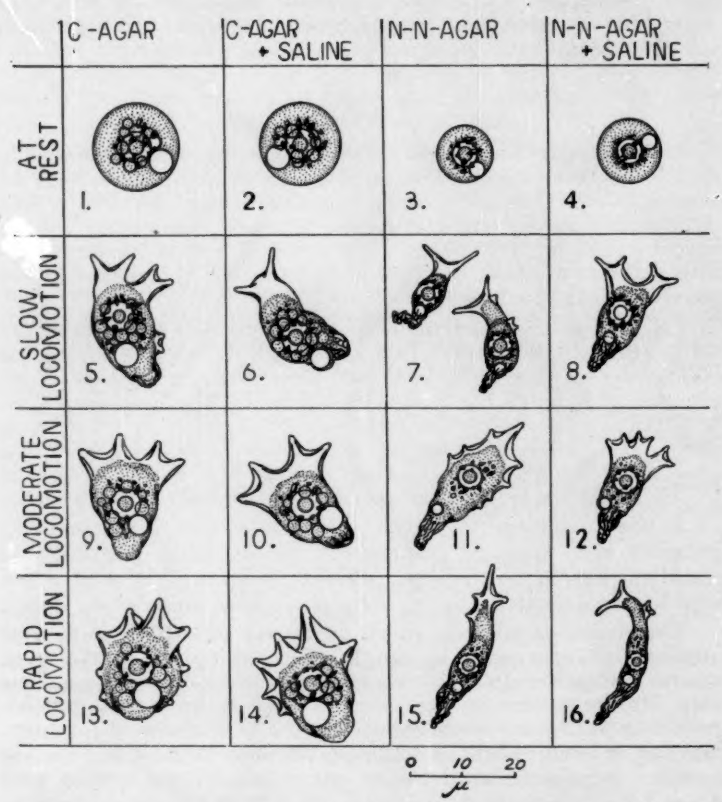
It was no surprise to observe that well-fed amebas on nutrient-cerophyll agar appeared plump, with many glistening globules of stored nutrients in the cytoplasm; whereas the less well-fed amebas and semi-starved animals on non-nutrient plates were progressively leaner.

The conical pseudopods, which are thrown forward in pairs, were approximately the same lengths in the well-fed and semi-starved amebas. However, the thickness of the pseudopods varied considerably. In the nutrient-cerophyll agar without liquid overlay, pseudopods extended by the amebas were 2 to 3 μ in diameter at the bases, tapering to rounded tips 1.5 to 2 μ in diameter (Figs. 5, 9, 13). On cerophyll agar with liquid overlay pseudopods of the amebas were 1.5 to 2.5 μ in diameter at the bases, and 1.25 to 1.5 μ in diameter at the rounded tips (Figs. 6, 10, 14).

On non-nutrient agar without liquid overlay, the amebas extended pseudopods which were 1.2 to 1.4 μ in diameter at the base and 0.8 to 1.0 μ in diameter at the tips (Figs. 7, 11, 15); on liquid-overlaid

non-nutrient agar, the amebas developed pseudopods 0.8 to 1.2 μ in diameter at the bases and 0.6 to 0.8 μ diameter at the tips (Figs. 8, 12, 16). In all cultures pseudopods measured 2 to 8 μ long, the longer pseudopods being slightly larger in diameter at bases and tips than were the shorter pseudopods (Figs. 11, 13, 14, 15, 16).

Some variation in size was noted for the more or less ovate bodily mass. This mass was usually broader, and blunter near the anterior wave and the rear in well-fed amebas (Figs. 13, 14). It was more slender and elliptical in semi-starved amebas, often with a somewhat



Figs. 1-4.—Resting forms of *Mayorella cultura* in the indicated media. Figs. 5-16.—Various locomotive forms on the indicated media. C — agar = nutrient agar with "cerophyll" extract; C — agar + saline = nutrient agar with "cerophyll" extract, overlaid with Neff's saline; n-n-agar = non-nutrient agar; n-n-agar + saline = non-nutrient agar overlaid with Neff's saline.

attenuated and wrinkled rear end, so that the starved amebas appeared longer (Figs. 7, 12, 15). Actual over-all length varied little, being 2 to 4 μ more for the starved amebas in rapid locomotion, due almost entirely to the attenuation of the contracted rear end.

The ratio of length/width, however, varied greatly for well-fed amebas *versus* semi-starved ones.

The average length/width ratio (all stages of locomotion) for the granular body mass, using the measurement of length from the rear end (at the base of the attenuated "tail," when present) to the border of the anterior clear portion from which pseudopods extend, divided by width at the broadest part of the granular bodily mass, was 1.42 for the well-fed amebas, and 2.20 for the semi-starving ones. Total length and total width were not employed, since pseudopods, in some stages of changing directional pathways, may be extended at both ends, or around the periphery (or a considerable portion thereof), producing less reliable measurement and ratio.

Giant forms occasionally appeared, usually on antibiotic-free, non-nutrient agar without overlay, when most of the amebas were encysted, and bacteria were available, but sparse. These giants were about 50 percent longer and broader than the average, otherwise normal in appearance and activity; but they did not encyst, and later died.

In locomotion the mayorellas progressed by throwing pseudopods forward in pairs above and to left or right (usually alternately) of the previously formed pair, so that a zig-zag, or wavy pathway was developed. One pseudopod of each pair was longer than the other, the longer one usually extended almost directly along the existing path of progress, the shorter at an angle usually between 60° to 90° to right or left of the existing pathway (Figs. 5, 6, 7). Older pairs of pseudopods themselves contracted, and were pulled laterally by contractions of the bodily mass, being reincorporated therein before the main part of the bodily mass passed their positions of adherence to the glass slide (Figs. 7, 13).

In slow movement, and in slow locomotion, the pseudopods of each pair were more nearly of the same lengths than in more rapid advance, and were less quickly contracted and reconstituted into the bodily mass (Figs. 10, 12).

Each pseudopod was connected to its partner of the pair by a clear web, of greater or lesser extent, particularly in more rapid locomotion (Figs. 11, 12, 13, 14).

In general, the more slender pseudopods of semi-starved amebas showed greater disparity of length between the two members of the pair than did the heavier pseudopods of the well-fed amebas (Figs. 15, 16). For the starved amebas in rapid locomotion the longer pseudopod directed along the pathway of locomotion measured 2 to 3 times as long as the shorter member directed angularly away from the locomotive path (Figs. 15, 16). Also, the angle between the bases of the pseudopods of the pair for the starved amebas was usually 70°

or more in spread, often as much as 90° (Fig. 15) and sometimes, in rapid advance, forming obtuse angles to 120° (Fig. 16). As a result such amebas appeared on cursory examination to be monopodal.

The well-fed amebas formed pseudopodal pairs which usually diverged from 60° - 80° (Figs. 9, 10) only occasionally as much as 90° (Figs. 6, 14), and were not seen to form obtuse angles. For both starved and well-fed amebas, those on the liquid-overlaid agar tended to throw pseudopodal pairs slightly more angularly divergent than their equivalently fed counterparts on non-liquid-overlaid surfaces. The clear web connecting the pseudopods of a pair rarely joined more than 5/8 the lengths of the newly-formed pseudopods of the well-fed amebas; but connected 2/3 to 3/4 of the lengths of such pseudopods of semi-starved ones, particularly in moderate locomotion (Figs. 11, 12). On liquid-overlaid media slightly more of the lengths of pseudopods of a pair were connected by the clear web then for amebas grown on non-liquid-overlaid agar (Figs. 10, 11, 12).

The rates of locomotion at 22°C. for the well-fed amebas were slower than those of the semi-starved mayorellas. In general, the well-fed amebas on cerophyll agar surfaces without liquid overlay moved slightly less than the over-all length of the body in one minute, averaging about 19 to 20 μ per minute when advancing steadily. Well-fed organisms on the cerophyll agar with liquid overlay moved a bit faster, 20 to 22 μ per minute, with frequent turns. Semi-starved amebas moved more rapidly forward, 25 to 28 μ per minute on non-overlaid agar, and 27 to 30 μ per minute on the liquid overlaid agar.

Severely-starved, emaciated amebas, conversely, moved very slowly, becoming very elongate, halting frequently before resuming progress. In short periods of steady advance only 8 to 12 μ would be traversed by such organisms per minute.

Locomotion by these mayorellid amebas was usually along the border of the streak where bacterial colonies were present. When several bacterial streaks were present on the same plate, little, if any, migration from one streak, or one colony along a streak, to another was evident, either by well-fed or poorly-fed amebas. In the few instances where amebas did wander away from the bacterial source, well-fed individuals soon extruded much of the stored globular materials, and encysted; while starved individuals which wandered away from the bacterial streaks became emaciated and inactive, and either died or formed small cysts.

Encystment occurred when there was a lack of bacteria available for food *in the immediate vicinity* of the ameba. On nutrient-cerophyll-agar plates the bacteria grew abundantly along the streaks where inoculated, and large numbers of amebas developed and migrated along the streak. Those which were prevented from reaching the bacteria for a few hours because of the dense aggregation of amebas, then encysted. Active trophic amebas were found, usually, no farther away from the bacteria than about 150 μ.

Excystment usually occurred when new colonies of bacteria de-

veloped, probably from bacterial spores in fecal wastes of the amebas among the clumps of cysts. It was under such situations that the "giant" amebas, previously mentioned, developed.

There appeared to be some correlation in nuclear volume and cytoplasmic volume. Resting, well-fed amebas (with many food globules) measured 16 to 18 μ in diameter in spherical form, the nucleus being spherical, 6.5 μ diameter, and the spherical nuclear endosome 3.2 μ diameter (Fig. 13). Semi-starved and newly excysted amebas measured 8 to 10 μ in spherical diameter, the nucleus being 3.5 μ diameter and the nuclear endosome 1.6 μ diameter (Figs. 15, 16.) When encysted, the spheroidal cytoplasmic mass was 8 μ diameter, the nucleus 3.2 μ diameter and the endosome about 1.5 μ diameter. Only one functional contractile vacuole appeared in any of the amebas under the various conditions employed.

In general, the major changes accompanying the progress of starvation were a loss in volume, more slender outlines in locomotion, and more slender, and slightly shorter pseudopods. The formation of pseudopods (and their conical, clear structure, rounded at tips) in pairs, more or less connected by a clear wave, did not change sufficiently to produce any error in the identity of the ameba as a species. Moreover, the pseudopods clearly were those characteristic of this species so long as the amebas moved about actively and fed successfully.

DISCUSSION

The fiction that the gross morphologies of any ameba and of its pseudopods are subject more to the vagaries of ecological conditions than to the metabolism of the organism perhaps began with the surface-tension theories of ameboid locomotion (Berthold, 1886; Bütschli, 1892; Rhumbler, 1898; Verworn, 1903); and failed to die with them. This fiction has been further perpetuated by Verworn's (*loc. cit.*) account of "changing" the "species" of ameba from "limax" to "radiosa" by addition of KOH to the water containing the organism. This fantastic misinterpretation by a great man of the results of his experiment has been regurgitated into most textbooks of protozoology as a warning against the employment of pseudopods and locomotive morphologies as taxonomic criteria for amebas (Calkins, 1926; Hyman, 1940; Jepps, 1956; Kudo, 1954; Minchin, 1912; Reichenow, 1953; Wenyon, 1926).

Environmental conditions supposed to be influential in obviating control by the ameba of its own morphology of bodily mass and pseudopodal forms include cations and anions, gross pH, O_2 and CO_2 tensions, light, temperature, pressure, and organic materials (particularly dissolved or colloidal, or as food).

Claims that gross form of the amebas (*i.e.* from "limax" to "radiosa") (Scheel, 1899) may be controlled at will by cations (Spek, 1925; Verworn, 1903) or that cations produce a monopodal form (Edwards, 1924), a contracted form (Brinley, 1928), or "Ca", "Mg" or "Ba" forms (Pantin, 1926) have been dismissed (Mast, 1928). Observations

show that locomotor processes in amebas are *not* dependent upon substances in solution in the water, but are regulated internally (Mast, *loc. cit.*). A radiate form is assumed in distilled water, or weak HCl at pH 5 to 6, in NaOH at pH 7.6 to 8, or in N/500 to N/100,000 concentrations of the chlorides and sulfates of Na^+, K^+, Ca^{++}, and Mg^{++}, or mixtures of these salts, in urea, and lactose solutions; followed *in each case* by a descent to the slide, then development of lobose, and, finally, monopodal ("limax") forms (Mast, *loc. cit.*). Other observations show that there are cycles of activity(Bovee, 1949) and growth (Bovee, 1953; Prescott and James, 1955) in a 24-hour period which produce similar sequential forms.

A like array of forms results from physical disturbance of the water and of the amebas (Bovee, 1953; Jennings, 1905; Mast, 1928; Schaeffer, 1921).

Low or high O_2 tensions cause rounding up, death and disintegration, except for brief exposures (Hulpieu, 1931) which cause the adoption of a temporary monopodal form. Increase of CO_2 similarly causes contraction and death, except in brief, non-lethal exposures (Reznikoff and Chambers, 1927); and injected bubbles of CO_2 gas cause some temporary damage followed by the assumption of the monopodal form (Reznikoff and Chambers, *loc. cit.*).

Temporary monopodal forms also develop in strong light (Prescott, 1956), or in low intensities of light (Mast and Stabler, 1937), sudden change of temperature (Hopkins, 1937b), weak direct electrical current (Angerer and Wilber, 1943), or starvation (Prescott, *loc. cit.*). After adjustment, or during and after feeding, lobose or discoidal forms reappear.

Severe experiments which approach lethality for the amebas result in a "rounding-up" of the ameba, followed by recovery if sub-lethal.

Centrifugation up to 149$\times$ gravity is followed by complete recovery (Murphy, 1940). High, hydrostatic pressures of 6,000 lbs./sq. in. are withstood, with recovery in 5 minutes (Marsland, 1956). Amputation of practically all the cytoplasm causes amebas to round up; but is often followed by complete recovery of specific identity (evidenced by normal movement and feeding) in 24 to 48 hours (Phelps, 1926; Prescott, 1956; Willis, 1916). Ultrasonic churning of the cytoplasm does not particularly disturb normal locomotion (Schmitt, 1929); and sublethal shocks of alternating current produce no permanent change (Angerer and Wilber, 1943); nor do sub-lethal vital stains (Torch, 1955); nor temperatures to 40° C. (Hopkins, 1937b; van Herwerden, 1927).

Lethal orders of salts (Brinley, 1928), HCl (Morita and Chambers, 1929), electric shocks (Englemann, 1869; Kuhne, 1864), high pressures (Marsland, 1956), and vital stains (Torch, 1955) all produce deformation, and/or coagulation and contraction to spherical form, destruction of the plasmalemma and disintegration. Surfactants tend to be toxic, and cause shrinkage of the bodily mass and pseudopods, plus blistering (Nardone, *et al.*, 1956).

In general, amebas respond to changes of a chemical or physical nature usually in one of three ways: (1) the assumption of a floating radiate stage; (2) the shift to a temporary monopodal form (usually characteristic of rapid locomotion); or (3) contraction to discoidal or spherical form reducing surface area. If the environmental change is sublethal, adjustment is made and normal activity resumed. If the environmental change is lethal, contraction, moribundity, death and disintegration follow.

Sublethal changes in the environment cause the assumption of a normal defensive morphological pattern. They do *not* materially nor permanently alter the nature of movement of the amebas nor their pseudopodal characteristics. In fact, any change in the coordinated pattern (Schaeffer, 1921) rate or type (Schaeffer, *loc. cit.;* Seifriz, 1939) of locomotion may be pathological. Form in coordinated locomotion is a criterion of normality (Schaeffer, *loc. cit.*; Seifritz, *loc. cit.*) and of taxonomic distinction (Bovee, 1949; Schaeffer, *loc. cit.*).

The surface over which the ameba moves is said by some observers to affect the form taken by an ameba (Hogue, 1917; Neff, 1958). Difficulty of attachment and movement have been noted on paraffin, quartz, and pyrex as compared to optical glass (Mast, 1928). "Walking" forms have been recorded (Bovee, 1953; Dellinger, 1906; Wilber, 1946), and other variations of movement on plant surfaces (Leidy, 1879; Penard, 1902). Density of agar in the culture medium is also said to affect form (Hogue, *loc. cit.*); as well as the depth of water film over the agar surface (Neff, *loc. cit.*). These observations, however, mostly represent experimental laboratory conditions and cannot obviate the facts that when crawling in water on a wet glass surface, (or any other surface) the patterns of locomotion adopted by any ameba on that type of surface are *characteristic of that ameba on that surface,* and of no other kind of ameba on that or any other surface.

Starvation affects mainly the size of the ameba (Andresen, 1956; Andresen and Holter, 1955; Johnson, 1930; Mast and Hahnert, 1935; Prescott, 1956) and perhaps the length of its pseudopods (Mast and Hahnert, *loc. cit.;* Short, 1946). Overfeeding affects principally the bodily size and relative diameter of pseudopods (Mast, 1939; Mast and Hahnert, *loc. cit.*). Kind of food, if adequate, has little if any effect on the pattern or the rate of locomotion (Hopkins, 1937a), but may produce temporary bipodal or monopodal forms (Short, *loc. cit.*), or a few more somewhat thinner and flatter pseudopods which are due more to the culture supplement (wheat or hay) then to the kind of food animal devoured by the ameba (Short, *loc. cit.*). No significant differences affecting bodily form result from digesting any one of a variety of food organisms, whether any one of them may be nutritionally adequate, inadequate, or toxic, so long as the amebas are able to move and feed (Andresen, *loc. cit.*; Mast and Hahnert, *loc. cit.*). Food taken by pinocytosis may affect bodily volume, but not form nor movement (Chapman, Andresen and Prescott, 1956).

It is highly important, as well as merely interesting, that in the

numerous papers written about experiments or studies on amebas very few of the observers or experimenters have noted any significant changes in form or activity of the amebas, so long as the conditions were sub-lethal.

It is doubly important that such changes were not reported, since they are exactly the criteria most sought for to determine experimental effects. Had such changes occurred, they are certain to have been seen and recorded; not overlooked, nor ignored, nor omitted.

In short, amebas react to and adapt to sub-lethal environmental changes, developing characteristic defensive morphological patterns which are a part of the adjustment; then, after a time, they resume normal and characteristic activity. Their adjustment to extra food is enlargement — in other words, they get "fat," and "clumsy." When starved they shrink and become lean ("monopodal") in locomotion.

So long as they are able to move in coordinated fashion (*i.e.* are not moribund) amebas retain and maintain their specifically identifiable bodily and pseudopodal morphologies, which are in turn related to and the result of their internally directed and coordinated metabolic and locomotive functions.

SUMMARY

Mayorella cultura Bovee (1960) has been grown in clonal cultures on media providing adequate nutrients for the bacteria serving it as food, and in bacteria-free clonal cultures in nutrient liquid media. It has also been maintained on non-nutrient media inadequate for either the bacterial or ameboid growth.

On the adequate media it becomes larger, and bulkier, with well-defined pseudopods; and on the inadequate media, emaciated. The characteristics of locomotive patterns are relatively undisturbed so long as the amebas are not moribund. It is concluded that locomotive patterns and pseudopodal forms are valid taxonomic criteria.

A survey of the literature concerning the effects of experimental and ecological conditions other than nutritive conditions indicates that for amebas, generally, these conditions do not particularly disturb the patterns of morphology and/or locomotion, so long as the experimental and ecological conditions are sublethal, and so long as the amebas are not moribund, and are able to move and feed in coordinated fashions. For amebas generally, as well as for *Mayorella cultura,* it is concluded that morphological patterns of the whole body and the pseudopods formed by it in locomotion are useful and valid taxonomic criteria.

REFERENCES

ANDRESEN, N. 1956. Cytological investigations on the giant amoeba, *Chaos chaos* L. *Compt. Rend. Trav. Lab. Carlsberg.,* **29**:435-555.

——— AND H. HOLTER 1945. Cytoplasmic changes during starvation of the amoeba *Chaos chaos* L. *Ibid., Ser. Chim.,* **25**:107-146.

ANGERER, C. A. AND K. M. WILBER 1943. The action of various types of electrical fields on the relative viscosity of plasmagel of *Amoeba proteus*. *Physiol. Zool.*, **16**:84-92.

BERTHOLD, G. 1886. *Studien über Protoplasmamechanik*. Leipzig, Engelmann. 332 pp., 7 pls.

BOVEE, E. C. 1949. Some observations on *Trichamoeba osseosaccus* Schaeffer. *Trans. Amer. Microscop. Soc.*, **70**:47-56.

———1953. Morphological identification of free-living amoebida. *Proc. Iowa Acad. Sci.*, **60**:599-615.

———1959. Studies on amebo-flagellates. I. The general morphology and mastigonts of *Trimastigamoeba philippinensis* Whitmore 1911. *Jour. Protozool.*, **6**:69-75.

———1960. A small ameba of freshwater lakes and ponds, *Mayorella cultura* n. sp. *Trans. Amer. Microscop. Soc.*, **79**: in press.

BRINLEY, F. J. 1928. The effect of chemicals on the viscosity of protoplasm as indicated by Brownian movement. *Protoplasma*, **4**:177-182.

BÜTSCHLI, O. 1892. *Untersuchungen über mikroscopische Schaume und das Protoplasma* . Leipzig, Engelmann. i-iv; 232 pp.; 6 pls.

CALKINS, G. N. 1907. The protozoan species. *Science*, N. S., **25**:697-698.

——— 1926. *The Biology of the Protozoa*. Philadelphia, Lea and Febiger. i-ix; 623 pp.

———1913. Genera and species of Amoeba. *Trans. 15th Internat. Cong. Hyd. Demog.*, **2**:287-305.

CHAPMAN-ANDRESEN, C. AND D. M. PRESCOTT 1956. Studies on pinocytosis in the amoebae *Chaos chaos* and *Amoeba proteus*. *Compt. Rend. Trav. Lab. Carlsberg, Ser. Chim.*, **30**:57-78.

DAUGHERTY, K. 1937. The action of anesthetics on amoeba protoplasm. *Physiol. Zool.*, **10**:473-483.

DELLINGER, O. P. 1906. Locomotion of amoebae and allied forms. *Jour. Exp. Zool.*, **3**:337-358.

EDWARDS, J. G. 1924. The action of certain reagents on amoeboid movement. II. Locomotion and physiological reactions. *Brit. Jour. Exp. Biol.*, **1**:571-595.

ENGELMANN, T. W. 1869. Beitrage zur Physiologie des Protoplasm. *Pflüg. Arch. ges. Physiol.*, **2**:307-322.

HALL, R. P. 1953. *Protozoology*. N. Y., Prentice-Hall. 682 pp.

HOGUE, M. J. 1917. The effect of media of different densities on the shape of amoebae. *Jour. Exp. Zool.*, **22**:565-572.

HOPKINS, D. L. 1926. The effect of hydrogen-ion concentration on locomotion and other life processes in *Amoeba proteus*. *Proc. Nat. Acad. Sci. U.S.A.*, **12**:311-315.

———1928. The effect of certain physical and chemical factors on locomotion and other life processes of *Amoeba proteus*. *Jour. Morph.*, **45**:97-119.

———1937a. The relations between food and locomotion (rate) and reproduction in the marine amoeba *Flabellula mira*. *Biol. Bull.*, **72**:334-343.

———1937b. The relation between temperature and locomotion in the marine amoeba *Flabellula mira* Schaeffer, with special reference to adaptation to temperature. *Protoplasma*, **28**:161-174.

HULPIEU, H. R. 1930. The effect of oxygen on *Amoeba proteus*. *Jour. Exp. Zool.*, **56**:321-362.

HYMAN, L. H. 1940. *The Invertebrates. Protozoa through Ctenophora*. New York: McGraw-Hill. i-xii; 726 pp.

JENNINGS, H. S. 1904. Movements and reactions of amoeba. *Publ. Carnegie* Inst., **16**: 129-134.

———1906. *Behavior of the Lower Organisms.* New York: Macmillan. i-xvi; 366 pp.

JEPPS, M. W. 1956. *The Protozoa, Sarcodina.* Edinburgh: Oliver and Boyd. i-vii; 183 pp.

JOHNSON, PERCY L. 1930. Reproduction in *Amoeba proteus. Arch. Protistenk.,* **71**: 463-498.

KRISZAT, G. 1952. Die Würking von Calcium auf Amöben (*Chaos chaos*). *Arkiv. Zool.,* **3**: 107-114.

KUDO, R. R. 1954. *Protozoology.* 4th ed. Springfield, Ill. Thomas. i-xi; 966 pp.

———1952. The genus *Pelomyxa. Trans. Amer. Microscop. Soc.,* **71**: 108-113.

———1959. *Pelomyxa* and related organisms. *Ann. N. Y. Acad. Sci.,* **78**: 474-486.

KUHNE, W. 1864. *Untersuchungen über das Protoplasma und die Contractiltat.* Leipzig., 158 pp.

LEIDY, J. 1879. Fresh-water rhizopods of North America. *U. S. Geol. Surv. Terr.,* **12**. Washington, D. C., Govt. Print. Office, i-xi; 323 pp., 57 pls.

MARSLAND, D. 1956. Protoplasmic contractility in relation to gel structure: Temperature-pressure experiments on cytokinesis and ameboid movement. *Intern. Rev. Cytol.,* **5**: 199-228.

MAST, S. O. 1928. Factors involved in changes of form in amoeba. *Jour. Exp. Zool.,* **51**: 97-120.

———1929. The mechanics of locomotion in *Amoeba proteus* with special reference to factors involved in attachment to the substratum. *Protoplasma,* **8**: 344-377.

———1939. The relation between kind of food, growth and structure in amoeba. *Biol. Bull.,* **77**: 391-398.

——— AND W. F. HAHNERT 1935. Feeding, digestion and starvation in *Amoeba proteus* (Leidy). *Physiol. Zool.,* **8**: 255-272.

——— AND N. STABLER 1937. The relation between luminous intensity, adaptation to light, and rate of locomotion in *Amoeba proteus* (Leidy). *Biol. Bull.,* **73**: 126-133.

MINCHIN, E. A. 1912. *An Introduction to the Study of the Protozoa.* London, Arnold. i-xi; 517 pp.

MORITA, Y-I, AND R. CHAMBERS 1929. Permeability differences between nuclear and cytoplasmic surfaces in *Amoeba dubia. Biol. Bull.,* **55**: 64-67.

MURPHY, Q. 1940. The effect of temperature on the viscosity of *Amoeba dubia* protoplasm. *Jour. Cell. Comp. Physiol.,* **16**: 401-404.

NARDONE, R. M., D. C. BRAUNGART, M. P. HURLEY, AND M. E. GIBSON 1956. The effect of surface-active agents on the permeability, survival, and pseudopod formation of *Pelomyxa carolinensis. Jour. Protozool.,* **3**: 119-121.

NEFF, R. J. 1957. Purification, axenic cultivation and description of a soil amoeba *Acanthamoeba* sp. *Ibid.,* **4**: 176-182.

———1958. Mechanisms of purifying amoebae on agar surfaces. *Ibid.,* **5**: 226-231.

NERESHEIMER, E. 1905. Ueber vegetative Kernveranderungen bei *Amoeba dolfleini* nov. sp. *Arch. Protistenk.,* **6**: 147-165.

PANTIN, C. F. A. 1926. On the physiology of ameboid movement. III. The action of calcium. IV. The action of magnesium. *Brit. Jour. Exp. Biol.,* **3**: 275-312.

PENARD, E. 1902. *Faune rhizopodique du bassin de Leman.* Geneva, Kundig. 714 pp.

PHELPS, L. A. 1926. Experimental analysis of the factors concerned in division of amoeba. *Trans. Amer. Microscop. Soc.,* **45**:133-145.

PRESCOTT, D. M. 1956. Mass and clone culturing of *Amoeba proteus* and *Chaos chaos. Compt. Rend. Trav. Lab. Carlsberg,* **30**:1-12.

——— AND T. W. JAMES 1955. Culturing *Amoeba proteus* on *Tetrahymena. Exptl. Cell Res.,* **8**:256-258.

RAY, D. L. AND R. E. HAYES 1954. *Hartmannella astronyxis* n. sp. of free-living amoeba. Cytology and life cycle. *Jour. Morph.,* **95**:159-188.

REICHENOW, E. 1953. *Lehrbuch der Protozoenkunde.* Sechste Auflage, begrundet F. Doflein. Jena, Fischer. 1213 pp.

REZNIKOFF, P. AND R. CHAMBERS 1927. Micrurgial studies in cell physiology. III. The action of CO_2 and some salts of Na, Ca and K on the protoplasm of *Amoeba dubia. Jour. Gen. Physiol.,* **10**:731-738.

RHUMBLER, L. 1898. Physikalische Analyse von Lebenserscheinungen der Zelle. I. Bewegung, Nahrungsaufnahme, Defekation, Vacuolen-Pulsation und Gehausbau bei lobosen Rhizopoden. *Arch. Entwicklungsmeck. Org.,* **7**:103-198.

SCHEEL, C. 1899. Beitrage zur Fortplanzung der Amoeben, in *Festschrift zum Siebenzigsten Geburtstag von Carl von Kuppffer,* Jena, Fischer. 569-580.

SCHAEFFER, A. A. 1916. Notes on the specific and other characters of *Amoeba proteus* Pallas (Leidy), *Amoeba discoides* spec. nov. *Arch. Protistenk.,* **37**:204-228.

———1920. *Amoeboid Movement.* Princeton, N. J., Princeton U. Press, i-vii; 156 pp.

———1926. Taxonomy of the amebas. *Carnegie Inst. Publ.,* **345**. Washington, D. C., Govt. Print. Office. 116 pp.; 12 pls.

SCHMITT, F. O. 1929. Ultrasonic manipulation. *Protoplasma,* **7**:332-340.

SEIFRIZ, W. 1939. Pathological changes in protoplasm. *Ibid.,* **32**:538-550.

SINGH, B. N. 1952. Nuclear division in nine species of small free-living amoebae and its bearing on the classification of the order Amoebida. *Phil. Trans. Roy. Soc. London., Ser. B.,* **236**:405-461.

SHORT, R. B. 1946. Observations on the giant amoeba, *Amoeba carolinensis* (Wilson, 1900). *Biol. Bull.,* **90**:8-18.

SPEK, J. 1925. Die protoplasmabewegung, ihre experimentelle Beeinflussing, und ihre theoretische Erklarung. *Hand. d. Normalen u. Pathologisch. Physiol.,* **8**:1-30.

TORCH, R. 1955. Cytological studies on *Pelomyxa carolinensis* with special reference to the mitochondria. *Jour. Protozool.,* **2**:167-177.

VAN HERWERDEN, M. A. 1927. Umkahrbare Gelatinierung durch Temperaturhöhung bei einer Susswasseramöbe. *Protoplasma,* **2**:271-277.

VERWORN, M. 1903. *Allgemeine Physiologie.* 4th ed. Jena, Fischer. 584 pp.

WENYON, C. M. 1926. *Protozoology.* New York, Wood. 1514 pp.; 20 pls.

WILBER, C. G. 1946. Notes on the locomotion of *Pelomyxa carolinensis. Trans. Amer. Microscop. Soc.,* **65**:318-322.

WILLIS, H. S. 1916. The influence of the nucleus on the behaviour of Amoeba. *Biol. Bull.,* **30**:253-270.

The Cyperaceae of Illinois.
I. Cyperus

ROBERT H. MOHLENBROCK
Southern Illinois University, Carbondale

This is the first in a series of studies concerning the family Cyperaceae in Illinois. It is intended to define the species within each group, to give synonymy, to supply keys for identification of the species, and to show distribution of the species in Illinois. Line drawings of the diagnostic characters of each group will be presented. In order of their appearance, the parts of the study will be: I. *Cyperus;* II. *Dulichium* and *Eleocharis;* III. *Bulbostylis, Fimbristylis, Fuirena, Hemicarpha,* and *Lipocarpha;* IV. *Scirpus* and *Eriophorum;* V. *Rhynchospora, Cladium,* and *Scleria;* and VI. *Carex.*

Herbaria which have made their collections of *Cyperus* available for this study are those of the Illinois State Museum (ISM), Illinois Natural History Survey (ILLS), Chicago Museum of Natural History (F), University of Illinois (ILL), Missouri Botanical Garden (MO), Eastern Illinois University (EI), Western Illinois University (WI), and Southern Illinois University (SIU). Much appreciation is accorded Mr. Don Drapalik who prepared the distribution maps and helped with the annotations.

History of the Genus

The genus *Cyperus* is a difficult group taxonomically which has rather poor species delimitation in Illinois as well as most of eastern United States. Many of the species show much variation, and considerable intergradation takes place among others.

Kükenthal has been an ardent student of *Cyperus,* and his monograph (1936) is foremost among those for the genus. Fernald and others, however, have pointed out numerous inconsistencies and errors so that Kükenthal's treatment should be studied critically before being followed.

Traditionally, *Cyperus* has been divided into other genera or subgenera based upon characteristics of the rhachilla, scales, number of stigmas, and achenes. The differences between some of the groups are rather difficult to observe and are based on somewhat tenuous characters.

Kükenthal recognizes six subgenera with only the subgenus *Juncellus* not being represented in the Illinois flora. Linnaeus (1753) listed several species of *Cyperus* to form the groundwork for future study of the genus. Other extensive works relating to North American species of *Cyperus* were by Rottboell (1773), Vahl (1806), Torrey (1836), Boeckeler (1868; 1870), Britton (1886), and Clarke (1883;

1884; 1898; 1903). In recent years, O'Neill's studies have contributed much to the present knowledge of North American species of *Cyperus*.

The name *Mariscus* has been applied to several species of rushes and sedges from the time it was first used by Pliny (77 A.D.) until Gaertner applied it to a group of plants which he related to the genus *Cyperus* in 1788. Since Vahl's work in 1806, *Mariscus* has been used as a subgenus of *Cyperus* or as a distinct genus, but this latter usage is prohibited since Zinn (1757) described a species belonging to *Cladium* under the genus *Mariscus*.

O'Neill (1942) has discussed thoroughly the reasons either for maintaining *Mariscus* as a subgenus of *Cyperus* or segregating it as a distinct genus.

The genus *Kyllinga*, created in 1773 by Rottboell and maintained in this rank by such workers as Vahl, Boeckeler, Clarke, and many recent authors (Jones, 1950; and others), was treated as a subgenus by Suringar in 1898, a rank which I propose to maintain for this taxon.

MORPHOLOGY OF THE ILLINOIS SPECIES

The species of *Cyperus* are cespitose annuals from fibrous roots or perennials with short rhizomes bearing corm-like swellings or with long scaly rhizomes (*C. esculentus*). In *C. esculentus*, the rhizomes sometimes give rise to edible swollen tubers. These tubers are frequently absent from herbarium specimens because they are easily lost in digging.

The culms range in size from depauperate specimens of *C. strigosus* which may be as small as one centimeter to robust specimens of *C. erythrorhizos* which may become nearly one-and-one-half meters tall. The culms may be wiry and very slender (*C. filiculmis* var. *macilentus*) or nearly one centimeter broad in several species. They are either glabrous or retrorsely scabrous beneath the inflorescence.

The leaves are flat or involute, rarely conduplicate, glabrous or sometimes scabrous on the margins, 0.5-12.0 mm broad, much surpassing or shorter than the culms.

The inflorescence, known as an anthela, is composed of 1-several sessile compact heads and frequently with 1-several simple or compound rays which may become 10 cm long. The inflorescence is subtended by 1-several involucral bracts, some of which usually greatly surpass the inflorescence. These bracts are flat or rarely involute, glabrous or scabrous along the margins.

The spikes may be cylindric, ellipsoid, oblongoid, or globose, with five to very numerous spikelets either radiating in all directions, horizontally spreading, ascending, or rarely reflexed (*C. lancastriensis*).

The spikelets are very flat to terete, linear to lanceolate, rarely falcate in some specimens of *C. erythrorhizos*, one- to forty-flowered, to 35 mm long, 1.0-3.5 mm broad, obtuse or subulate.

Scales vary in color from stramineous to strongly marked with

purple, loosely to tightly imbricate, or with the scales remote in *C. engelmannii,* narrowly oblong, lanceolate, ovate, or rotund (*C. houghtonii*), obtuse to acute or acuminate and outwardly recurved in *C. acuminatus* and *C. aristatus,* sometimes mucronulate or with a mucro to 1.5 mm long, obscurely or conspicuously one- to fifteen-nerved, 1-5 mm long. The rhachilla which is occasionally exposed between the scales may be broadly winged or wingless.

There are 1-3 stamens per flower. The stigmas are two- or three-cleft, sometimes nearly to the base, frequently early deciduous, rarely persistent and protruding up to 4 mm in *C. diandrus.*

The achenes are lenticular or trigonous, rarely flattened, stramineous to fuscous to black, narrowly linear to broadly ovate, sometimes with tranverse wrinkles (*C. flavescens*) or minutely pebbled (*C. aristatus*), obtuse or apiculate, 0.5-3.3 mm long.

GEOGRAPHICAL CONSIDERATIONS

Kükenthal (1936), summarizing the geographical distributions of *Cyperus,* listed 40 species from Atlantic North America of which 18 were known from Illinois. (The nineteenth Illinois species, *C. grayioides,* which recently has been described, was unknown of course to Kükenthal).

The majority of the Illinois species has a general distribution in northeastern North America from Maine to the Dakotas, south to Texas and Florida. Included here are *C. diandrus, C. pseudovegetus, C. engelmanii, C. lancastriensis, C. ovularis,* and *C. filiculmis.* The same pattern of distribution with an extension into the tropics and into Europe is found in *C. flavescens, C. esculentus,* and *C. densicaespitosus. C. filicinus* is known from the eastern seaboard and from an inland Illinois station.

Species with a distribution throughout continental United States are *C. erythrorhizos, C. ferruginescens,* and *C. strigosus.* An extension of this pattern into Mexico and South America is the distribution of *C. rivularis* and *C. aristatus.*

The remaining four species show a more limited distribution. *Cyperus acuminatus* basically is a western species ranging eastward to Indiana. *Cyperus schweinitzii* and *C. houghtonii* are northern species which include northern Illinois as a southern limit to their ranges. *Cyperus grayioides* is an endemic of the sandy regions of the Illinois River in Mason and Whiteside Counties.

In Illinois, *C. strigosus, C. erythrorhizos, C. esculentus,* and *C. ferruginescens* are common throughout the entire state, frequently becoming weedy. *Cyperus acuminatus* and *C. aristatus* are found sparingly throughout Illinois.

Cyperus pseudovegetus and *C. densicaespitosus* have limited ranges in the southern counties. The former has been recorded only from a few stations north to Wayne County while the latter is known only as far north as Jackson County.

Cyperus ovularis and *C. flavescens* have nearly identical ranges in Illinois, although the latter is much rarer. Both occur in the extreme southern counties with one station recorded from Peoria County. It is probable that neither occur any longer in Peoria County where they have not been found since Brendel's collections during the latter half of the nineteenth century.

Cyperus rivularis is mostly northern in its Illinois distribution, although it is known from St. Clair and Pope Counties. *Cyperus diandrus* is localized in a few northern counties, mostly those bordering the Illinois River, and in Jackson County along the Mississippi River.

Cyperus schweinitzii is found in counties of the northern one-third of Illinois, but is also adventive along a railroad in Jackson County. *Cyperus filiculmis* var. *filiculmis* has a natural range in Illinois similar to *C. schweinitzii*. *Cyperus filiculmis* var. *macilentus* is more widespread, although it is uncommon in the southern counties.

The remaining five species are very rare in Illinois: *Cyperus lancastriensis* from two extreme southern counties (Pulaski and Massac); *C. filicinus* from a roadside ditch in Jackson County where it is possibly adventive; *C. engelmannii* with a disjunct range which includes Lake, McHenry, St. Clair, Union, and Alexander counties; *C. houghtonii* from a railroad in Cook County, and the endemic *C. grayioides* from Mason and Whiteside counties.

Ecological Considerations

The Illinois species of *Cyperus* fall into three basic habitat types — sand, low moist ground along bodies of water, and dry fields and bluffs.

Those species which occupy the river banks are subject to frequent inundations which seem to affect their morphology. Many dwarfed and out-of-season specimens are encountered in this habitat.

Cyperus aristatus appears to have the greatest range of tolerance. It is most abundant in low ground, although it is not uncommon in moist depressions atop sandstone bluffs in the southern counties.

Several species reach weedy proportions. *Cyperus esculentus* is very abundant in cultivated fields while *C. strigosus* is a common inhabitant of deserted fields. Even *C. densicaespitosus* is growing rampant in a lawn in Carbondale (Jackson County).

Systematic Treatment

CYPERUS L. Sp. Pl. ed. 1:44. 1753.

Eucyperus Rikli *in* Pringsheims Jahrb. 27:568. 1895.
Pycreus P. Beauv. Fl. Oware. 2:48. 1807.
Mariscus Gaertn. De Fruct. et Semin. 1:12. 1788.
Kyllinga Rottb. Descr. et Icon. 12. 1773.
Torulinium Desv. *in* Ham., Prodr. Pl. Ind. Occ. 15. 1825.

NATURAL KEY TO THE ILLINOIS SPECIES OF CYPERUS

A. Rhachilla of spikelets continuous; scales gradually deciduous from base of rhachilla to apex.
  B. Stigmas 3; achene trigonous .... Subgenus I. *Cyperus*
  B. Stigmas 2; achene lenticular, compressed to biconvex .... Subgenus II. *Pycreus*
A. Rhachilla of spikelets articulated; scales persistent and then falling all at once from the rhachilla.
  C. Rhachilla not separating into joints.
    D. Stigmas 3; achene trigonous .... Subgenus III. *Mariscus*
    D. Stigmas 2; achene lenticular .... Subgenus IV. *Kyllinga*
  C. Rhachilla articulate at base of each scale .... Subgenus V. *Torulinium*

SUBGENUS I. *Cyperus.*

A. Spikelets disposed on an elongated rhachis.
  B. Spikes cylindric; wings of the rhachilla colored. (Section *Fastigiati*) .... 1. *C. erythrorhizos*
  B. Spikes ovate to broadly turbinate; wings of the rhachilla hyaline. (Section *Esculenti*) .... 2. *C. esculentus*
A. Spikelets on a very short rhachis. (Section *Luzuloidei*).
  C. Perennial; achene linear-oblong .... 3. *C. pseudovegetus*
  C. Annual; achene ellipsoid .... 4. *C. acuminatus*

SUBGENUS II. *Pycreus.*

A. External cells of the achene of isodiametric hexagons.
  B. Scales scarcely sulcate. (Section *Polystachyi*) .... 5. *C. filicinus*
  B. Scales strongly sulcate. (Section *Sulcati*).
    C. Styles cleft nearly to the middle .... 6. *C. rivularis*
    C. Styles cleft nearly to the base .... 7. *C. diandrus*
A. External cells of the achene rectangular-oblong (Section *Flavescentes*) .... 8. *C. flavescens*

SUBGENUS III. *Mariscus.*

A. Spikelets flat or compressed.
  B. Achene linear-oblong. (Section *Strigosi*) .... 9. *C. strigosus*
  B. Achene elliptic-oblong to oblong-ovate.
    C. Plants annual; stamens 1 or 2. (Section *Aristati*) .... 10. *C. aristatus*
    C. Plants perennial; stamens 3. (Section *Laxiglumi*).
      D. All the spikelets ascending .... 11. *C. schweinitzii*
      D. Spikelets divergent.
        E. Spikes ovate; achene as broad as long .... 12. *C. houghtonii*
        E. Spikes globose or hemispherical; achene longer than broad.
          F. Spikes hemispherical; scales mostly acute, approximate .... 13. *C. filiculmis*
          F. Spikes globose; scales obtuse, spreading .... 14. *C. grayioides*
A. Spikelets subterete. (*Section Umbellati*).
  G. Spikelets reflexed in an obovoid head .... 15. *C. lancastriensis*
  G. Spikelets radiating in all directions in a globose head .... 16. *C. ovularis*

SUBGENUS IV. *Kyllinga.*

17. *Cyperus densicaespitosus* of Section *Kyllinga* is our only representative.

SUBGENUS V. *Torulinium.*

Our only representatives belong to Section *Feraces.*

A. Scales approximate, overlapping ....18. *C. ferruginescens*

A. Scales remote, the tip of one barely reaching the base of the one above it ....19. *C. engelmannii*

ARTIFICIAL KEY TO THE ILLINOIS SPECIES OF CYPERUS

A. Achenes lenticular; stigmas 2.
  B. Spikelets 1-flowered; inflorescence of 1-3 sessile heads; plants with a strong sweet odor ....17. *C. densicaespitosus*
  B. Spikelets 5- to 35-flowered; inflorescence of 1-several radiating sessile spikelets and usually 1-several rays; plants essentially inodorous.
    C. Achenes black, nearly as broad as long, with transverse wrinkles; scales stramineous ....8. *C. flavescens*
    C. Achenes drab or gray, longer than broad, without transverse wrinkles; scales usually suffused with purple.
      D. Styles cleft nearly to base, persistent and conspicuously exserted to 4 mm from scales ....7. *C. diandrus*
      D. Styles cleft to about middle, early deciduous, included or projecting to 2 mm from scales.
        E. Scales closely imbricate, strongly suffused with purple (scales stramineous in *C. rivularis* f. *elutus*) ....6. *C. rivularis*
        E. Scales with tips somewhat spreading, the spikelets appearing serrate, stramineous or purple only on the margins ......5. *C. filicinus*

A. Achenes trigonous; stigmas 3.
  F. Scales with strongly reflexed acuminate tips ....10. *C. aristatus*
  F. Scales with tips either appressed or slightly spreading.
    G. Spikes spherical or globose, with spikelets radiating in all directions.
      H. Scales appressed but with the tips shortly excurved; spikes to 8 mm across.
        I. Perennial; achene narrowly lanceolate to linear ....3. *C. pseudovegetus*
        I. Annual achene oblong ....4. *C. acuminatus*
      H. Scales appressed to spreading, their tips straight; some of the heads over 1 cm across.
        J. Scales appressed; spikelets 2- to 3-flowered ....16. *C. ovularis*
        J. Scales spreading; spikelets 5- to several-flowered ......14.*C. grayioides*
    G. Spikes hemispherical, cylindrical, ellipsoidal, or lanceolate, but not globose or spherical.
      K. Spikelets arising from a central axis.
        L. Scales with a mucro 0.5-1.5 mm long; achenes 2.2-3.3 mm long ....11. *C. schweinitzii*
        L. Scales merely acute or with a mucro to 0.5 mm long; achenes usually 1.2-2.1 mm long.
          M. Achenes 1.2-1.5 mm long, 1.2-1.5 mm broad; spikelets nearly all ascending ....12. *C. houghtonii*
          M. Achenes 1.2-2.1 mm long, 0.8-1.1 mm broad; some of the spikelets spreading or slightly reflexed ....13. *C. filiculmis*
      K. Spikelets produced pinnately along the axis.
        N. Scales 1.0-1.5 mm long; achene 0.8-1.0 mm long ....1. *C. erythrorhizos*

N. Scales 1.5-4.5 mm long; achene 1.0-2.8 mm long.
O. Scales very remote, the tip of one just reaching the base of the one above it, giving the spikelet a zigzag appearance ....19. *C. engelmannii*
O. Scales approximate and overlapping.
P. Some or all of the mature spikelets reflexed; spikelets subterete ....15. *C. lancastriensis*
P. None of the spikelets (except sometimes the lowest pair) reflexed; spikelets flattened.
Q. Rhizomes scaly and usually ending in a tuber; scales at the tips of the spikelets rather blunt, giving the spikelet an obtuse appearance ....2. *C. esculentus*
Q. Rhizomes absent or merely becoming hard and corm-like.
R. Plants annual; scales ferruginous or golden-brown; achenes obovoid-oblong, 1.0-1.7 mm long ....18. *C. ferruginescens*
R. Plants perennial; scales stramineous; achenes linear, 1.3-2.2 mm long ....9. *C. strigosus*

1. CYPERUS ERYTHRORHIZOS Muehlenb. Descr. Gram. 20. 1817. (Fig. 1).

Cyperus halei Torr. ex Britt. *in* Bull. Torrey Club 13:213. 1886.

Cyperus erythrorhizos var. *halei* (Torr.) Kükenth in Kükenth., Pflanzenr. 20:59. 1936.

Annual from fibrous, often red, roots; culms to 1.3 meters tall, occasionally dwarfed to 1 cm tall, smooth; leaves to 10 mm wide, shorter than to equalling the culm, with scabrous margins and with the lower sheaths usually purplish near the base; inflorescence of 1-several sessile spikes and numerous simple or compound rays, with up to 8 involucral bracts, most of which surpass the inflorescence; spikes cylindric with numerous horizontally spreading or ascending spikelets; spikelets falcate, 6- to 36-flowered, 3-20 mm long, with closely imbricated scales; scales reddish-brown with stramineous margins, rarely stramineous throughout, with a green midrib, broadly lanceolate, mucronate, faintly nerved, 1.0-1.5 mm long; stamens 2 or 3; styles 3; rhachilla winged; achene trigonous, ovoid, gray or whitish, 0.8-1.0 mm long, about 0.5 mm wide.

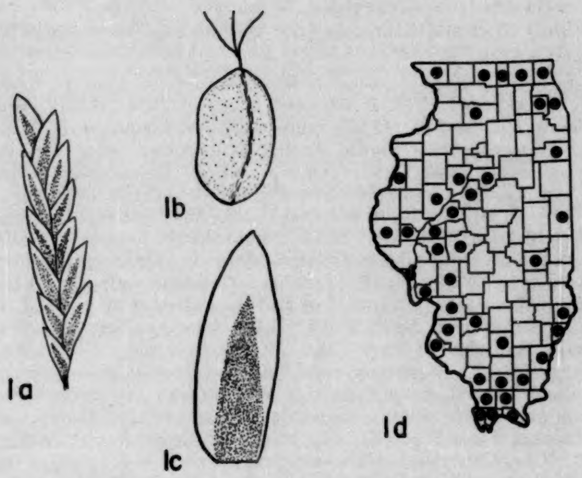
Habitat.—Moist, often sandy soil.

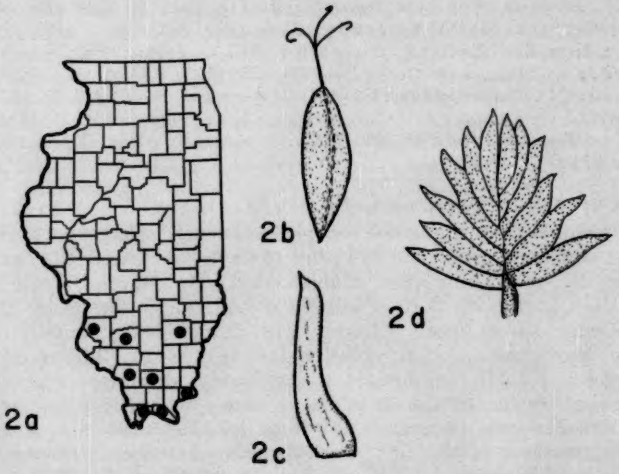
Range.—Massachusetts to Washington south to California and Florida.

Cyperus erythrorhizos is readily distinguished by its tiny reddish-brown scales and gray or whitish achenes which are 0.8-1.0 mm long.

Great variation occurs within the species. Some specimens from Jackson County (*Mohlenbrock 10010*) measured 1.3 meters tall and bore so great an inflorescence that the entire plants toppled to the ground. Specimens as small as 1 cm may be found along river banks which are inundated frequently.

Specimens over 8 dm tall and with spikelets 3-5 mm long have been referred to *Cyperus halei* (or *C. erythrorhizos* var. *halei*), but complete intergradation among entities makes it impossible to main-





Figs. 1 and 2. 1.—*Cyperus erythrorhizos.* a. Spikelet, x 5. b. Achene, x 20. c. Scale, x 30. d. Map. 2.—*Cyperus pseudovegetus.* a. Map. b. Achene, x 20. c. Scale, x 15. d. Spikelet, x 5.

tain *halei* either as a species or a variety. *Ahles 6975* from Pulaski County is only 8 cm tall and bears spikelets 3-5 mm long, but is merely a dwarfed, suppressed form.

Whiting 1802 and *Miller s.n.* are specimens with the scales entirely stramineous.

Specimens Examined: ADAMS: Goose Lake N. of Quincy, *Evers* 15168 (ILLS). ALEXANDER: T17S, R16W, sect. 8, *Evers* 32828 (ILLS). BOONE: W. of Belvidere, *Fell* 541210 (ISM). BROWN: E. of Cooperstown, *Evers* 40562 (ILLS). CALHOUN: N. of Hardin, *Evers* 20420 (ILLS). CASS: One mile S. of Beardstown, *Evers s.n.* (ILLS). CLINTON: SE. of Germantown, *Evers* 20599 (ILLS). COLES: Lake Mattoon, *Stover s.n.* (EI). COOK: N. of Harvey, *Winterringer* 1593 (ILL). DUPAGE: Wheaton, *Fuller* 1949 (ISM). FULTON: Nine miles SE. of Canton, *Miller s.n.* (ILLS). HENDERSON: Oquawka, *Patterson s.n.* (SIU). JACKSON: Near Grand Tower, *Collins s.n.* (SIU). JEFFERSON: E. of Waltonville, *Evers* 52307 (ILLS). JERSEY: Pere Marquette State Park, *Fuller* 541 (ISM). JO DAVIESS: SE. of East Dubuque, *Evers* 49241 (ILLS). JOHNSON: E. of Grantsburg, *Evers* 36015 (ILLS). KANE: Elgin, *Benke s.n.* (F). KANKAKEE: Kankakee, *Hill s.n.* (ILL). LAKE: Two miles NE. of Barrington, *Bennett s.n.* (ILLS). LAWRENCE: SE. of Lawrenceville, *Winterringer* 13492 (ISM). LEE: SE. of Amboy, *Evers* 41003 (ILLS). MCHENRY: Ringwood, *Vasey, s.n.* (ILL). MACOUPIN: Macoupin, *Robertson* 9236 (ILLS). MADISON: E. of Madison, *Evers* 8050 (ILLS). MASON: Swamp, *Rexroat* 1207 (ISM). MASSAC: Near University of Illinois camp, *Fuller* 1802 (SIU). MENARD: Athens, *Hall s.n.* (F). MONROE: S. of Fults, T4S, R10W, *Bailey & Swayne* 2806 (SIU). MORGAN: NE. of Meredosia, *Rexroat* 2195 (ISM). PEORIA: Illinois River, *McDonald* 61½ (ILL). PULASKI: N. of Grand Chain, *Ahles* 6975 (ILL). ST. CLAIR: Fish Lake, *Eggert s.n.* (MO). SALINE: N. of Mitchellsville, *Winterringer s.n.* (ISM). SANGAMON: Clear Lake, *Fuller* 9597 (ISM). TAZEWELL: Near East Peoria, *V. Chase* 3301 (ILL). UNION: Pine Hills swamp, *Stieglitz s.n.* (SIU). VERMILION: Near Danville, *Bock & V. Chase* 2301 (ILL). WABASH: Mt. Carmel, *Schneck* 60 (ILL). WHITE: S. of Mill Shoals, *Ahles* 6635 (ILL). WILLIAMSON: Crab Orchard Lake, *Fuller* 2404 (ISM). WINNEBAGO: Rockford, *Fell* F48-393 (ISM). WOODFORD: Along Illinois River, *V. Chase* 21440 (ILL).

2. CYPERUS ESCULENTUS L. Sp. Pl. 45. 1753.

Perennial from numerous conspicuously scaly rhizomes terminating in a small hard tuber; culms rather stout, to one meter tall, smooth; leaves flat, to 10 mm wide; inflorescence with 1-several sessile spikes and 1-10 rays, with 3-10 broad involucral bracts surpassing the inflorescence; spikes mostly cylindric, with numerous horizontally radiating or ascending spikelets; spikelets flattened, 6- to 30-flowered, 6-35 mm long, 1.5-3.0 mm broad; scales loosely imbricate or spreading somewhat, ovate, obtuse to acute or rarely with the terminal scale acuminate, 7- to 11-nerved, 2-3 mm long, stramineous or golden brown, scarious at the tip; rhachilla winged; achenes oblongoid to narrowly oblongoid, 1.2-1.8 mm long, 0.4-0.8 mm broad, brownish or grayish.

Habitat.—Moist, frequently cultivated soil.

Range.—Maine to Washington south to Arizona and Florida; Mexico; tropical America; Europe.

Two varieties may be separated as follows:

a. Inflorescence simple to compound; spikelets to 15 mm long, 1.5-3.0 mm broad; scales loosely or usually closely imbricate, obtuse, or the terminal mucronulate; achene obovoid ....*C. esculentus* var. *esculentus*

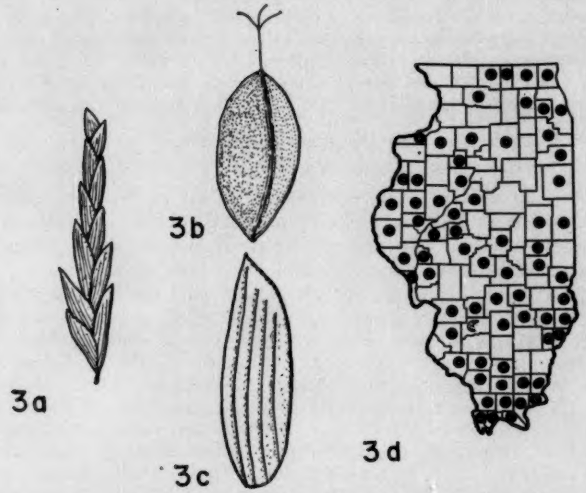
a. Inflorescence compound; spikelets longer and narrower, 20-35 mm long and less than 1.5 mm broad; scales loosely imbricate, mucronulate; achenes narrowly oblongoid ....*C. esculentus* var. *leptostachyus*

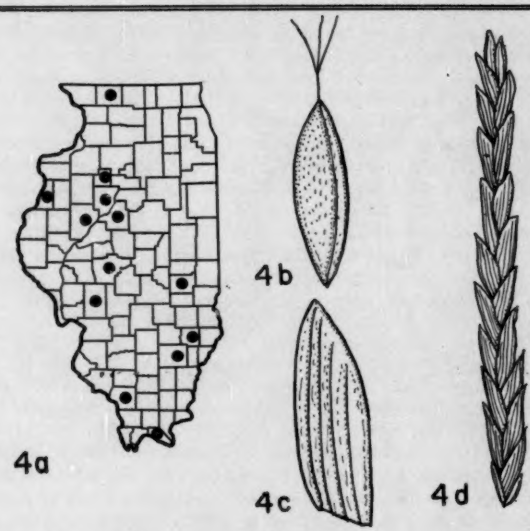
2a. *Cyperus esculentus* var. *esculentus* (Fig. 3).

Cyperus phymatodes Muehlenb. Descr. Gram. 23. 1817 (in part).

The typical variety is a troublesome weed in recently cultivated ground throughout Illinois. The common name of Nut-grass is from the presence of tubers at the ends of the rhizomes. The presence of scales on the rhizomes readily identifies this species.

Specimens Examined: ADAMS: N. of Quincy, *Evers* 15191 (ILLS). ALEXANDER: Three and one-half miles N. of Olive Branch, *Evers* 18693 (ILLS). BOND: SE. of Hookdale, *Evers* 48861 (ILLS). BOONE: Near Caledonia, *Fell* 54952 (ISM). BUREAU: E. of Mineral, *Evers* 21201 (ILLS). CALHOUN: Pere Marquette Wildlife Research Area, *Muller* 9743 (ILLS). CASS: River bank, *Rexroat* 1116 (ISM). CHAMPAIGN: Waste ground, University of Illinois, *Gibbs* 28615 (ILL). CHRISTIAN: Taylorville, *Andrews s.n.* (ILL). CLARK: S. of Marshall, *Evers* 19741 (ILLS). CLAY: Flora, *Amman* 14618 (ILLS). CLINTON: *Evers* 12484 (ILLS). COLES: Humboldt, *Amman* 14620 (ILLS). COOK: River Forest, *Moffatt* 265 (ILL). CRAWFORD: NW. of Hutsonville, *Evers* 19757 (ILLS). DOUGLAS: N. of Arcola, *Winterringer* 3492 (ISM). DUPAGE: Wheaton, *Fuller* 1906 (ISM). EDWARDS: W. of Albion, *Evers* 20174 (ILLS). EFFINGHAM: One mile NE. of Effiingham, *Evers* 5743 (ILLS). FAYETTE: S. of St. Elmo, *O'Dell* 44 (ILL). FRANKLIN: One mile S. of Rand City, *Evers* 52389 (ILLS). FULTON: N. of Lewiston, *Evers* 14913 (ILLS). GALLATIN: ½ mile S. of Ridgway, *G. Dillard s.n.* (SIU). GREENE: SE. of Greenfield, *Evers* 20703 (ILLS). HANCOCK: NW. of Bowen, *Evers* 26981 (ILLS). HARDIN: Elizabethtown, *Evers* 11290 (ILLS). HENDERSON: E. of Shakoken, *Evers* 18343 (ILLS). HENRY: E. of Atkinson, *Evers* 21178 (ILLS). IROQUOIS: E. of Milford, *Ahles* 3158 (ILL). JACKSON: Grand Tower, *Fuller & Fisher* 271 (ISM). JOHNSON: SW. of Forman, *Evers* 19921 (ILLS). KANE: Elgin 3663 (F). KANKAKEE: Six miles W. of Kankakee, DeSelm 413 (F). LAKE: Libertyville, *Mathins s.n.* (ILL). LASALLE: Starved Rock State Park, *Werner* 9797 (ILLS). LAWRENCE: One-half mile E. of Sumner, *Sivert* 107 (ILL). MCDONOUGH: N. of Bushnell, *Myers* 1170 (ISM). MCHENRY: Near Algonquin, *Nason* 20760 (ILL). MACON: Two miles S. of Niantic, *Clokey* 2448 (ILL). MACOUPIN: Carlinville, *Fuller* 2259 (ISM). MADISON: E. of Madison, *Evers* 14097 (ILLS). MARION: Near Patoka, *Winterringer* 3498 (ISM). MASON: Four miles S. of Easton, *Robinson* 12399 (ISM). MASSAC: Brookport, *Fuller & Welch* 348 (ISM). MENARD: Athens, *Hall* 29400 (ILL). OGLE: Rock River, *Moffatt* 460 (ILL). PEORIA: Peoria, *McDonald s.n.* (ILL). PIKE: N. of Florence, *Evers* 20300 (ILLS). POPE: N. of Eddyville, *Mohlenbrock* 10011 (SIU). PULASKI: Douglas Landing, *Evers* 41453 (ILLS). RANDOLPH: Four miles SW. of Prairie du Rocher, *Trojcak* 3084 (ISM). RICHLAND: Four miles N. of Olney, *Shaw* 691 (ISM). ROCK ISLAND: SW. of Hillsdale, *Evers* 21101 (ILLS). ST. CLAIR: Near French Village, *Neill* 913 (ISM). SALINE: Harrisburg, *Stout* 9805 (ILLS). SANGAMON: Clear Lake, *Fuller* 8832 (ISM). SCHUYLER: Two and one-half miles SW. of Beardstown, *Rexroat* 2318 (ISM). SCOTT: Four miles W. of Winchester, *Flynn* 14302 (ISM). SHELBY: Shelby-





Figs. 3 and 4. 3.—*Cyperus esculentus* var. *esculentus*. a. Spikelet, x 4. b. Achene, x 20. c. Scale, x 15. d. Map. 4.—*Cyperus esculentus* var. *leptostachyus*. a. Map. b. Achene, x 15. c. Scale, x 15. d. Spikelet, x 3.

ville, *Fisher s.n.* (EI). STARK: S. of Bradford, *Evers* 21234 (ILLS). TAZEWELL: Mackinaw, *Stillman* 9803 (ILLS). UNION: Wolf Lake, *Fuller & Fisher* 780 (ISM). VERMILION: Between Oakwood and Collison, *G. Jones* 12999 (ILL). WABASH: Near Sportsman's Park, *Schneck s.n.* (ILL). WARREN: W. of Monmouth, *Evers* 20988 (ILLS). WASHINGTON: Five miles W. of Ashley, *Boewe* 14621 (ILLS). WILL: Lockport, *Hill* 3137 (ILL). WILLIAMSON: Crab Orchard Lake, *S. Abney & G. Dillard* 29 (SIU). WINNEBAGO: Rockford, *Fell & Fell* 147-380 (ISM).

2b. *Cyperus esculentus* var. *leptostachyus* Boeckl. Linnaea 36:290. 1870. (Fig. 4).

Cyperus phymatodes Muehlenb. Descr. Gram. 23. 1817.
Cyperus esculentus f. *angustispicatus* (Britt.) Fern. Rhodora 44: 151. 1942.

This variety, with larger and narrower spikelets, has achenes which average longer and narrower than those in var. *esculentus.*

Specimens Examined: COLES: One mile NW. of Oakland, *Voigt* 918 (SIU). FULTON: Canton, *Wolf s.n.* (F). HENDERSON: Oquawka, *Patterson s.n.* (ILL). JACKSON: Fountain Bluff, *Cranwill s.n.* (ILL). MACOUPIN: Carlinville, *Robertson* 9762 (ILLS). MASSAC: Five miles E. of Brookport, *McCree* 348 (SIU). PEORIA: Near Farmington, *V. Chase* 4732 (ILL). RICHLAND: Sugar Creek prairie, *Ridgway* 255 (F). ST. CLAIR: Indian Lake, Eggert *s.n.* (F). SANGAMON: Clear Lake, *Fuller* 6256 (ISM). STARK: Near Wady Petra, *V. Chase* 1542 (ILL). STEPHENSON: Near Redott, *Fell* 52905 (ISM). TAZEWELL: Pekin, *V. Chase* 19858 (ILL). WAYNE: E. of Fairfield, *Walker* 50 (ILL).

3. CYPERUS PSEUDOVEGETUS Steud. Synops. Cyper. 24. 1855. (Fig. 2).

Cyperus virens Gray, Manual ed. 2:493. 1856, non. Michx.

Perennial from a short rhizome; culms 35-65 cm tall, glabrous; leaves 2-4 mm wide, usually equalling the culm, glabrous; inflorescence of 1-several sessile heads and numerous compound rays; spikes with numerous radiating spikelets; spikelets 5- to 13-flowered, 3.0-6.5 mm long, with rather loosely arranged scales; scales narrow, subacute, with slender excurved tips, 1.8-2.2 mm long, faintly-nerved, pale greenish-yellow; stamen 1; style 3-cleft; achenes linear, 1.0-1.4 mm long, stipitate, stramineous.

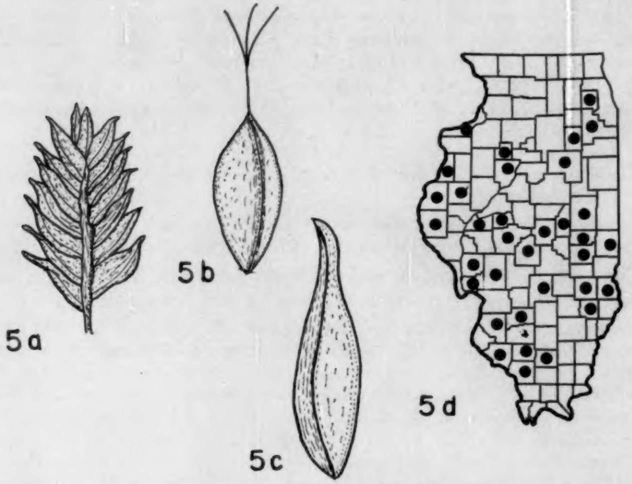
Habitat.—Moist soil.

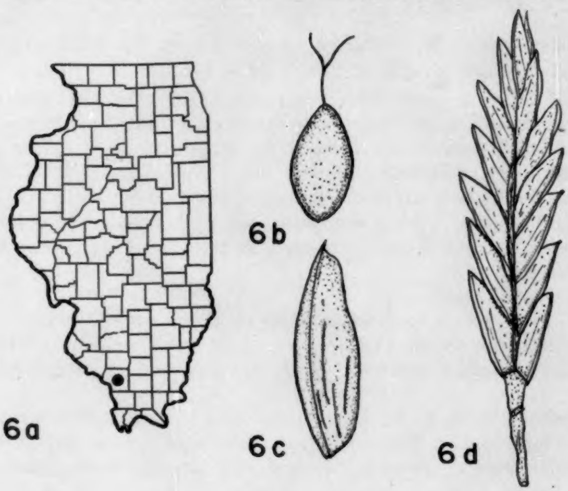
Range.—New Jersey to Kansas south to Texas and Florida.

This sedge is one of the rarer species of *Cyperus* in Illinois. It has been collected in eight counties, all in the southern one-third of the state.

It is related closely to *C. acuminatus* which it resembles strongly. *Cyperus pseudovegetus,* however, is a perennial which grows considerably taller than *C. acuminatus* and also has narrower scales and achenes.

Specimens Examined: JACKSON: Carbondale, *V. H. Chase* 9978 (ILL). MASSAC: Metropolis, *H. C. Benke* 4700 (F). PULASKI: S. of Ullin, *R. A. Evers* 19998 (ILLS). ST. CLAIR: Wet places, *H. Eggert s.n.* (F). WABASH: N. of Mt. Carmel, *W. Bailey & J. R. Swayne s.n.* (SIU) WASHINGTON: Venedy Station, *Evers* 33946 (ILLS). WAYNE: Five miles N. of Cisne, *Winterringer* 3446 (ILLS). WILLIAMSON: Crab Orchard Lake, *Evers* 18629 (ILLS).





Figs. 5 and 6. 5.—*Cyperus acuminatus*. a. Spikelet, x 6. b. Achene, x 25. c. Scale, x 20. d. Map. 6.—*Cyperus filicinus*. a. Map. b. Achene, x 15. c. Scale, x 15. d. Spikelet, x 3.

4. CYPERUS ACUMINATUS Torr. & Hook. Ann. Lyc. N. Y. 3:435. 1836. (Fig. 5).

Cespitose annual with fibrous roots; culms 4-35 cm tall, usually stramineous; leaves few, 1-2 mm wide, nearly equalling or slightly exceeding the culm; involucral bracts 2-4, exceeding the inflorescence, the longest to 8 cm, 1-2 mm wide; inflorescence of numerous spikes 1-2 cm in diameter, borne on rays 1-4 cm long, usually with one or more sessile spikes; spikelets flattened, ovate to oblong, rarely linear, ascending or spreading, closely imbricated, 12- to 40-flowered; scales ovate, acute, outwardly curved at the tip, 1.8-2.6 mm long, pale, with one conspicuous central nerve and usually 2-4 very obscure lateral ones; stamen 1; style cleft; achenes ellipsoid to oblongoid, pointed at either end, 0.5-1.0 mm long, 0.5 mm broad, much surpassed by the scales, stramineous.

Habitat.—Wet ground.

Range.—Indiana to North Dakota south to Texas and Florida; Washington, Oregon.

Cyperus acuminatus resembles *C. aristatus* in its recurved scales, but those of *C. aristatus* are much more recurved. *Cyperus acuminatus* lacks the Slippery Elm aroma so characteristic of *C. aristatus.*

Specimens Examined: ADAMS: Melrose, *Brinker* 3568 (ISM). ALEXANDER: McClure, *Cranwill s.n.* (ILL). CHAMPAIGN: Near Champaign, *Burrill & Seymour* 18574 (ILL). CHRISTIAN: Taylorville, *Andrews s.n.* (ILL). CLINTON: Between Carlyle and Shattuc, *Ahles* 6056 (ILL). COLES: N. of Mattoon, *Stover s.n.* (EI). CRAWFORD: Between Oblong and Stoy, *Ahles* 4946 (ILL). DOUGLAS: Arcola, *Mohr* 9723 (ILLS). DUPAGE: *Hawkins* 9724 (ILLS). EDGAR: W. of Paris, *Evers* 7354 (ILLS). FAYETTE: Near Pecan Island, *O'dell* 591 (ILL). FRANKLIN: N. of Benton, *Ahles* 5532 (ILL). GREENE: N. of Eldred, *Evers* 20324 (ILLS). GRUNDY: SW. of Gardner, *Evers* 21684 (ILLS). HANCOCK: Augusta, *Mead s.n.* (MO). HENDERSON: Near Oquawka, *Patterson s.n.* (ILL). JACKSON: S. of Murphysboro, *Hardy & Voigt* 128 (ISM). JASPER: Newton, *Boewe* 9729 (ILLS). JERSEY: Kemper, *McDonald s.n.* (ILL). LIVINGSTON: SW. of Cayuga, *Evers* 21712 (ILLS). MCDONOUGH: S. of Bushnell, *V. Chase* 11500 (ILL). MACON: Decatur, *Clokey* 1080 (MO). MACOUPIN: One mile S. of Hettick, *Winterringer* 3487 (ISM). MARION: W. of Brubaker, *Evers* 20649 (ILLS). MASON: *Brendel s.n.* (ILL). MENARD: Athens, *Hall s.n.* (MO). PEORIA: "West Bluff," Peoria, *McDonald s.n.* (ILL). PERRY: S. of Pyatts, *Evers* 18725 (ILLS). PIATT: N. of Monticello, *Ahles* 6566 (ILL). RANDOLPH: Between Chester and Evansville, *Ahles* 5666 (ILL). RICHLAND: Three and one-half miles N. of Olney, *Shaw* 729 (ISM). ROCK ISLAND: E. of Cordova, *Evers* 35499 (ILLS). ST. CLAIR: Cahokia, *Neill* 1363 (ISM). SANGAMON: Springfield Township, *Carter* 14370 (ISM). STARK: Near Wady Petra, *V. Chase* 682 (ILL). WASHINGTON: Nashville, *French* 3023 (SIU). WILL: Lockport, *Hill s.n.* (ILL).

5. CYPERUS FILICINUS Vahl, Enum. 2:332. 1806. (Fig. 6).

Annual from fibrous roots; culms to 30 cm tall, smooth; leaves to 3 mm wide, shorter than the culm, smooth; inflorescence of 1-2 sessile heads and 1-3 rays to 6 cm long, with 3-6 involucral bracts, some normally exceeding the inflorescence; spikes with up to 10 spikelets

radiating in all directions; spikelets very flat, linear-lanceolate, acute, 12- to 25-flowered, to 25 mm long, 3 mm broad; scales broadly lanceolate, stramineous or golden brown, acute, mucronulate, 2.0-3.5 mm long; stamens 2; styles deeply 2-cleft; achenes narrowly obovoid, obtuse at summit, 1.2-1.6 mm long, brownish.

Habitat.—Wet, usually brackish soils.

Range.—Maine to Florida and Louisiana; West Indies.

The discovery of this east coast sedge in a roadside ditch in southern Illinois in 1950 has come as a complete surprise. Because of the roadside habitat, it would appear to be adventive except that all its associates at this station (*Carex lanuginosa, Juncus tenuis,* etc.) are part of the native wet ditch flora of southern Illinois.

Specimen Examined: JACKSON: Roadside ditch along Highway 51, N. of DeSoto, *Voigt* 391 (SIU).

6. CYPERUS RIVULARIS Kunth, Enum. 2:6: 1837. (Fig. 7).

Annual from fibrous roots; culms to 50 cm tall, smooth; leaves to 3 mm broad, nearly equalling the culm, smooth; inflorescence of 1 or 2 sessile heads and usually with 1-5 rays to 8 cm long, with 3 (-4) involucral bracts much exceeding the inflorescence; spikes with up to 10 spikelets radiating in all directions; spikelets very flat, blunt, 8- to 35-flowered, to 25 mm long and 4 mm broad; scales closely imbricated, ovate, obtuse, 2.0-2.5 mm long, strongly colored red-brown from near the mid-vein to the margins, or rarely merely stramineous; stamens 2 or rarely 3; styles 2-cleft to about the middle, early deciduous; achenes narrowly obovate, 1.0-1.5 mm long, 0.5-0.8 mm broad, chestnut or grayish.

Habitat.—Wet ground along banks and shores.

Range.—Maine to South Dakota south to Texas and Georgia; California; Mexico.

Three forms recognizable in Illinois may be separated as follows:

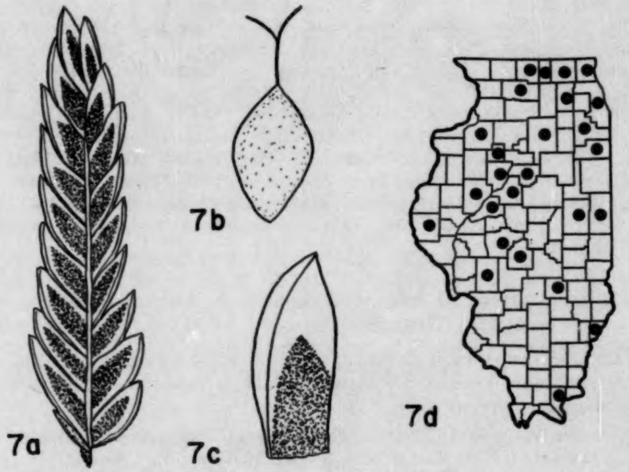
a. Scales strongly suffused with red-brown or purple pigmentation.
  b. Culms to 30 cm tall .... *C. rivularis* f. *rivularis*
  b. Culms (30-) 40-50 cm tall .... *C. rivularis* f. *elongatus*
a. Scales stramineous throughout, except for the greenish midrib .... *C. rivularis* f. *elutus*

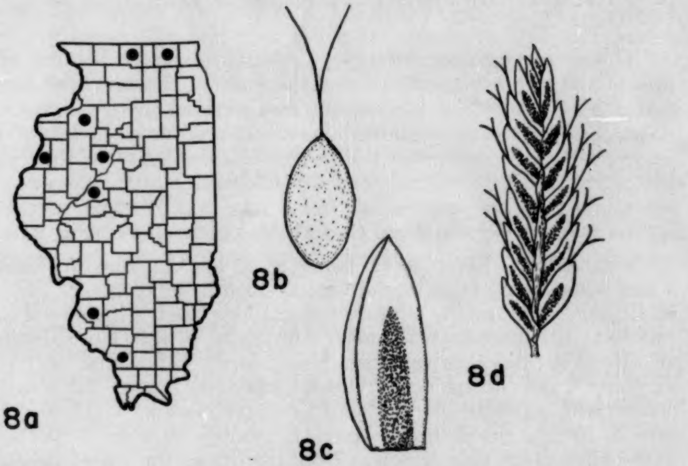
6a. *Cyperus rivularis* f. *rivularis*

Cyperus diandrus Torr. var. *castaneus* Torr. *in* Ann. Lyc. N.Y. 3:252. 1836.

The typical form is rather abundant in northern and central Illinois where it grows along rivers and the edges of ponds and lakes. It is extremely rare in the southern counties.

Specimens Examined: ADAMS: Eight miles SE. of Quincy, *Brinker* 3020 (ISM). BOONE: Kishwaukee River, *E. W. Fell* 52783 (ISM). CHAMPAIGN: Urbana, *Clinton* 28612 (ILL). CHRISTIAN: Taylorville, *Andrews s.n.* (ILL). COOK: Grand Crossing, Chicago, *A. Chase* 2004 (ILL). EFFINGHAM: Nine miles S. of Effingham, *Winterringer* 8994 (ISM). FULTON: *Clinton* 28737





Figs. 7 and 8. 7.—*Cyperus rivularis.* a. Spikelet, x 3. b. Achene, x 20. c. Scale, x 15. d. Map. 8.—*Cyperus diandrus.* a. Map. b. Achene, x 15. c. Scale, x 15. d. Spikelet, x 2.

(ILL). HENRY: Near Colma, *E. W. Fell & G. B. Fell* 46833 (ISM). KANE: Trout Park, Elgin, *Fuller* 9299 (ISM). KANKAKEE: St. Anne, *Graham* 1907 (ISM). LAKE: Illinois Beach State Park, *Winterringer* 8975 (ISM). LASALLE: Starved Rock State Park, *Ries* 7547 (ISM). MCHENRY: Three miles NW. of Ringwood, *Fuller* 13311 (ISM). MACOUPIN: Carlinville, *Robertson* 9731 (ILLS). MASON: Havana, *Fuller* 1839 (ISM). OGLE: Rock River, *Moffatt* 459 (ILL). PEORIA: Near Peoria, *Brendel s.n.* (ILL). POPE: Lake Glendale, *Bailey & Swayne* 3017 (ISM). SANGAMON: Salisbury, *Fuller* 7941 (ISM). STARK: *V. Chase s.n.* (ILL). TAZEWELL: Near Spring Mills, *V. Chase* 3314 (ISM). VERMILION: Kickapoo State Park, *Ahles* 1782 (ISM). WABASH: Near Patton, *Schneck s.n.* (ILL). WILL: Braidwood, *Graham* 9938 (ISM). WINNEBAGO: Rockford, *Fuller s.n.* (ISM). WOODFORD: Spring Bay, *V. Chase* 10100 (ILL).

6b. *Cyperus rivularis* f. *elongatus* Boeckl. *in* Linnaea 35:453. 1868 (pro. var.).

The tall form which at maturity may reach a height of 50 cm, has a very strikingly slender appearance. It is rare in Illinois where it grows with the typical form.

Specimens Examined: COLES: Three miles E. of Charleston, *Stover s.n.* (EI). TAZEWELL: Near East Peoria, Spring Mill Bay, *V. Chase* 9042 (ILL).

6c. *Cyperus rivularis* f. *elutus* C. B. Clarke *in* Journ. Linn. Soc. 21:65. 1884.

This form curiously resembles *Cyperus flavescens* because of the lack of red-brown pigmentation of the scales. However, the achenes of f. *elutus* are usually 1.2-1.5 mm long and narrowly obovate while those of *C. flavescens* are about 1 mm long and broadly obovate.

Specimens Examined: COLES: Three miles E. of Charleston, *Stover* 437-A (EI). WABASH: Mt. Carmel, *Schneck s.n.* (ILL).

7. CYPERUS DIANDRUS Torr. Cat. Pl. N. Y. 90. 1819. (Fig. 8).

Annual from fibrous roots; culms to 40 cm tall, smooth; leaves to 3 mm wide, nearly equalling the culm, smooth; inflorescence of 1 or 2 sessile heads and usually 1-5 rays to 6 cm long, with 3 involucral bracts exceeding the inflorescence; spikes with up to 10 spikelets radiating in all directions; spikelets very flat, blunt, 5- to 35-flowered, to 25 mm long and 4 mm broad; scales closely imbricated, ovate, 2-3 mm long, obtuse, with a reddish-purple band along the margins which sometimes extends to near the midrib; stamens 2 or rarely 3; styles 2-cleft nearly to the base, protruding to 4 mm from the tips of the scales, persistent; achene narrowly obovoid, 1.0-1.5 mm long, somewhat more than half as broad.

Habitat.—Wet ground along banks and shores.

Range.—New Brunswick to North Dakota south to New Mexico and South Carolina.

Much confusion exists in the separation of *C. diandrus* from *C. rivularis.* Many Illinois specimens called *C. diandrus* are actually *C.*

rivularis, a fact which greatly restricts the known range of *C. diandrus* in Illinois.

Separation based on the red-brown pigmentation of the scales is not too reliable. Whether the style is cleft to the middle, or to the base, is difficult to determine frequently due to the fragility of the styles. The most easily observed difference is that the styles of *C. diandrus* project to 4 mm from the scales and are persistent; the styles of *C. rivularis* are included within the scales or project to only 2 mm and are rarely deciduous.

C. diandrus is known in Illinois from a few stations mostly in the northern counties.

Specimens Examined: HENDERSON: Oquawka, *Patterson s.n.* (F). HENRY: N. side of Penny Slough, *Dobbs* 19498 (ILLS). JACKSON: Along Mississippi River near Grand Tower, *S. Abney & G. Dillard* 270 (SIU). MCHENRY: Algonquin, *Nason s.n.* (ILL). MASON: *Ahles* 29403 (ILL). PEORIA: Peoria, *Brendel s.n.* (ILL). ST. CLAIR: Bank of the Mississippi River, *H. Eggert s.n.* (MO). WINNEBAGO: Rockford, *E. W. Fell s.n.* (ISM).

8. CYPERUS FLAVESCENS L. Sp. Pl. 46. 1753. (Fig. 9).

Cyperus poaeformis Pursh, Fl. Am. Sept. 1:50. 1814.
Cyperus flavescens var. *poaeformis* (Pursh) Fern. Rhodora 41:529. 1939.

Cespitose annual; roots fibrous; culms 8-45 cm tall, straw-colored, rarely becoming purplish near the base, smooth, 0.5-1.5 mm broad; leaves 0.5-2.0 mm wide, about one-half to two-thirds as long as the culms; bracts usually 3, rarely 2-4, at least one and sometimes all of them exceeding the inflorescence, the longest to 12 cm, 0.5-2.0 (rarely to 3.0) mm broad; spikes crowded into condensed umbels or occasionally with 1-3 rays up to 3 cm long; spikelets very flat, 12- to 25-flowered, 5-15 mm long, 2.0-3.0 mm broad, obtuse at the tip; scales pale yellowish-brown, ovate, obtuse, with broad hyaline margins, distinctly green-keeled, 1.5-2.5 mm long; stamens 3; styles deeply 2-cleft; achene flattened, obovate, with minute transverse wrinkles, 0.8-1.0 mm long, nearly as broad, apiculate, black.

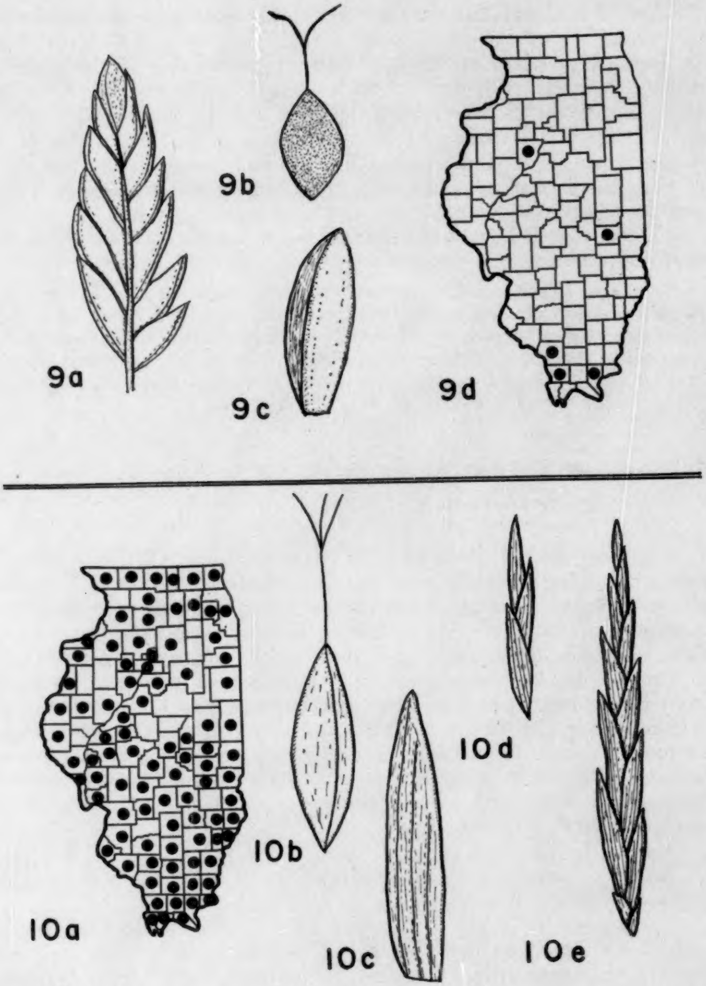
Habitat.—Wet open soil.

Range.—Massachusetts to Michigan south to Texas and Florida; tropical America; Europe.

A comparative study of *Cyperus flavescens* from the Old World with North American material reveals no reason to consider the New World specimens varietally distinct. *Montpellier* 3957 from Pyranée, France, for example, is totally indistinguishable from United States material.

Cyperus flavescens is exceedingly rare in Illinois. It is most common in the extreme southern counties, although there is a collection of it from Peoria County. This species very closely resembles *C. rivularis* f. *elutus,* but may be distinguished on the basis of the achene.

Specimens Examined: COLES: Rock Park, *Stover s.n.* (EI). JACKSON: Mid-



Figs. 9 and 10. 9.—*Cyperus flavescens*. a. Spikelet, x 4. b. Achene, x 15. c. Scale, x 15. d. Map. 10.—*Cyperus strigosus*. a. Map. b. Achene, x 15. c. Scale, x 10. d-e. Spikelets, x 4.

land Hills Country Club, *Voigt* 2928 (SIU). PEORIA: Peoria, *Brendel s.n.* (ILL). POPE: Lake Glendale, *Bailey & Swayne* 3016 (SIU). UNION: Cobden, collector unknown.

9. CYPERUS STRIGOSUS L. Sp. Pl. 47. 1753. (Fig. 10).

Cyperus stenolepis Torr. Ann. Lyc. N.Y. 3:263. 1836.

Cyperus strigosus f. *robustior* Kunth, Enum. 2:88. 1837.

Cyperus strigosus var. *robustior* (Kunth) Britt. Bull. Torr. Club 13:212. 1886.

Cyperus strigosus var. *stenolepis* (Torr.) Kükenth. *in* Fedde, Rep. 23:189. 1926.

Perennial from a hard corm-like rhizome; culms to 1.2 m tall, smooth; leaves flat, to 12 mm wide, some of them surpassing the culms; inflorescence with 1-2 sessile heads and 2-12 simple or compound rays, with several of the numerous bracts much longer than the inflorescence; spikes cylindric, with numerous horizontally radiating or ascending spikelets; spikelets strongly flattened, 3- to 25-flowered, to 30 mm long, with appressed or loosely ascending scales; scales acute and often mucronulate, 3.5-5.0 mm long, 7- to 11-nerved, golden-brown, with scarious margins; rhachilla winged; achene linear to linear-oblongoid, 1.3-2.2 mm long, 0.4-0.7 mm broad.

Habitat.—Wet ground.

Range.—Quebec to South Dakota south to Texas and Florida; west coast of the United States.

Cyperus strigosus is one of our most variable species with every degree of intergradation occurring among several characters. Very robust specimens with appressed scales (f. *robustior*) or loosely arranged scales (var. *stenolepis*) occur, but intergradations of all degrees may be found from the smallest to the largest variations. It does not seem feasible to retain any of the named variations.

Cyperus strigosus occurs in very moist soil probably in every county of Illinois.

Specimens Examined: ADAMS: Three miles E. of Ursa, *Brinker* 2964 (ILL). ALEXANDER: N. of Tamms, *Evers* 15506 (ILLS). BOND: S. of Greenville, *Winterringer* 12982 (ISM). BOONE: W. of Belvedere, *E. W. Fell* 54897 (ISM). BUREAU: E. of Mineral, *Evers* 21199 (ILLS). CALHOUN: NW. of Belleview, *Evers* 41243 (ILLS). CASS: Eight miles SW. of Beardstown, *Winterringer* 5247 (ISM). CHAMPAIGN: Mahomet, *Seymour* 18593 (ILL). CHRISTIAN: Taylorville, *Andrews s.n.* (II). CLARK: S. of Marshall, *Winterringer* 7041 (ISM). CLAY: Clay City, *Ahles s.n.* (ILL). CLINTON: N. of Beckemeyer, *Evers* 14303 (ILLS). COLES: E. of Charleston, *Stover s.n.* (EI). CRAWFORD: NW. of Hutsonville, *Evers* 19758 (ILLS). CUMBERLAND: SW. of Casey, collector unknown, (ILLS). DEKALB: Kingston, *Evers* 19121 (ILLS). DOUGLAS: Near Tuscola, *Fuller* 12046 (ISM). DUPAGE: Wheaton, *Fuller* 1906 (ILLS). EDGAR: W. of Paris, *Evers* 7353 (ILLS). EDWARDS: Five miles S. of Albion, *Evers* 31637 (SIU). EFFINGHAM: SE. of Watson, *Evers* 48200 (ILLS). FAYETTE: Two miles SE. of Ramsey, *Fuller* 14000 (ISM). FRANKLIN: S. of Logan, *Evers* 41383 (ILLS). FULTON: Canton, collector unknown, (ILL). GALLATIN: Three miles N. of Omaha, *Evers* 19899 (ILLS). GREENE: W. of Carrollton, *Winterringer* 13030 (ISM). HAMILTON: E. of Piopolis, *Evers* 13136

(ILLS). HANCOCK: Carthage, *Gates* 10002 (ILL). HARDIN: E. of Karber's Ridge, *Evers* 8516 (ILLS). HENDERSON: Crystal Lake, *Hawkins* 9801 (ILLS). HENRY: Seven miles N. of Geneseo, *Evers* 35512 (ILLS). IROQUOIS: sandy region, *Tehon* 9806 (ILLS). JACKSON: Giant City State Park, *Mohlenbrock s.n.* (SIU) JEFFERSON: S. of Mt. Vernon, *Ahles* 5492 (ILL). JERSEY: Pere Marquette State Park, *Fuller* 2030 (ISM). JO DAVIESS: S. of Blanding, *Evers* 35756 (ILLS). JOHNSON: E. of Vienna, *Winterringer* 7042 (ISM). KANE: Elgin, *Sherff* 1806 (ILL). KANKAKEE: Kankakee, *Schultes s.n.* (ILL). LAKE: East Zion, *Brown* 117 (ILL). LASALLE: Starved Rock State Park, *Ries* 7546 (ISM). LAWRENCE: SW. of Birds, *Evers* 19793 (ILLS). LEE: Two miles E. of Kingdom, *Keithley* 293 (ISM). LIVINGSTON: SW. of Cayuga, *Evers* 21693 (ILLS). MCDONOUGH: S. of Bushnell, *V. Chase* 11506 (ILL). MCHENRY: Algonquin, *Nason s.n.* (ILL). MACON: Lake Decatur, *Winterringer* 6534 (ISM). MACOUPIN: N. of Bunker Hill, *Winterringer* 12987 (ISM). MADISON: Near Livingston, *Winterringer* 13168 (ISM). MARION: Near Patoka, *Winterringer s.n.* (ISM). MARSHALL: S. of Lacon, *Evers* 19598 (ILLS). MASON: Havana, *Fuller* 1836 (ISM). MASSAC: E. of Joppa, *Evers* 36485 (ILLS). MENARD: Three miles E. of Oakford, *Evers* 12990 (ILLS). MONROE: SE. of Poe, *Evers* 20505 (ILLS). MONTGOMERY: S. of Litchfield, *Evers* 14060 (ILLS). MORGAN: Three miles NE. of Meredosia, *Rexroat* 2061 (ISM). MOULTRIE: NW. of Sullivan, *Winterringer* 9156 (ISM). OGLE: Four miles E. of Oregon, *Fuller* 9277 (ISM). PEORIA: Peoria, *McDonald s.n.* (ILL). PERRY: One mile S. of Tamaroa, *Winterringer* 9421 (ISM). PIATT: Monticello, *G. Jones* 18912 (ILL). PIKE: N. of Florence, *Evers* 20309 (ILLS). POPE: Belle Smith Springs, *Evers* 52607 (ILLS). PULASKI: N. of Pulaski, *Mohlenbrock & Voigt* 5549 (SIU). PUTNAM: Lake Senachwine, *V. Chase* 10801 (ILL). RANDOLPH: One and one-half miles N. of Prairie du Rocher, *Trojcak* 3162 (ISM). RICHLAND: Lower Wabash valley, *Ridgway* 1212 (ILL). ROCK ISLAND: S. of Cordova, *Evers* 13927 (ILLS). ST. CLAIR: N. of Mascoutah, *Evers* 20570 (ILLS). SALINE: Sahara Lake, *S. Abney & G. Dillard* 85 (SIU). SANGAMON: Rochester, *Fuller* 5478 (ISM). SCOTT: Four miles W. of Winchester, *Flynn* 14302 (ISM). SHELBY: SW. of Lakewood, *Evers* 35931 (ILLS). STARK: Wady Petra, *V. Chase* 1208 (ILL). STEPHENSON: Three miles W. of Seward, *E. Fell* 52822 (ISM). TAZEWELL: S. of Pekin, *E. Fell* 5 (ISM). UNION: S. of Jonesboro, *Winterringer* 11998 (ISM). VERMILION: Danville, Kickapoo State Park, *Miller s.n.* (ILL). WABASH: Near Mt. Carmel, *Schneck s.n.* (ILL). WASHINGTON: Irvington, *French s.n.* (SIU). WAYNE: Near Cisne, *Carter* 14084 (ISM). WHITE: SW. of Carmi, *Evers* 19888 (ILLS). WHITESIDE: Sinnissippi Park, Sterling, *V. Chase* 12937 (ILL). WILL: Braidwood, *Graham* 9932 (ISM). WILLIAMSON: Crab Orchard Lake, *Hardy* 50 (SIU). WINNEBAGO: Rockford, *E. Fell* 52-807 (ISM). WOODFORD: Four miles S. of Spring Bay, *V. Chase* 6216 (ISM).

10. CYPERUS ARISTATUS Rottb. Descr. & Icon. 6:23. 1773. (Fig. 11).
Cyperus inflexus Muehlenb. Descr. Gram. 16. 1817.
Cyperus aristatus var. *inflexus* (Muehlenb.) Boeckl. Linnaea 35:500. 1868.

Cespitose annual with an odor of *Ulmus rubra;* roots fibrous, forming a dense mat; culms 3-15 cm tall, very slender, purplish-tinged at base, smooth; leaves 2-3 on each culm, 0.5-1.5 mm wide; involucral bracts 2-4, all exceeding the inflorescence, the longest to 8 cm, 0.5-2.0 mm broad; spikes crowded into a sessile head-like cluster, occasionally with a few on rays up to 2.5 cm long; spikelets flattened, 6- to 18-

flowered, 3-9 mm long, 1-2 mm wide; scales oblong to oblong-lanceolate, prominently 7- to 9-nerved, 1-2 mm long with an outwardly curving acuminate tip 0.5-1.0 mm long, green when young becoming reddish-brown or brown at maturity; rhachilla wingless; stamen 1; style 3-cleft, deciduous; achenes trigonous, obovoid, minutely pebbled, 0.5-1.0 mm long, 0.3-0.5 mm broad, pale brown.

Habitat.—Moist soil along rivers, around lakes, or in fields.

Range.—Throughout most of North America, Mexico, South America.

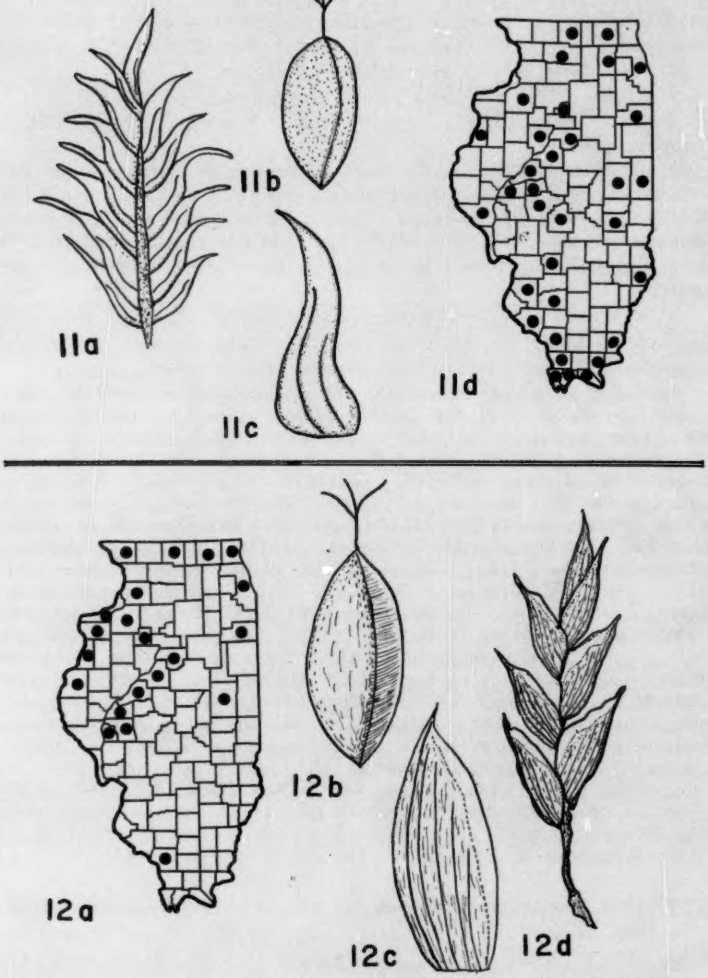
Kükenthal (1936), on the basis of somewhat shorter spikes and somewhat larger achenes, considers this species as a variety of the Old World *Cyperus aristatus* while Gleason (1952) makes no distinction between the two. O'Neill (1942) has amassed considerable data to show that the New World specimens are not distinct from Rottboell's entity.

This species is scattered throughout Illinois in moist situations, particularly along the larger rivers. It occurs in moist depressions atop exposed sandstone bluffs in the southern counties.

Specimens Examined: ALEXANDER: W. of Sandusky, *Ahles* 4713 (ILL). BOND: Near Belvidere, *E. Fell* 54-1139 (ISM). CASS: Beardstown, *Rexroat* 3480 (ISM). CHAMPAIGN: Urbana, *Ahles* 6298 (ILL). CHRISTIAN: Taylorville, *Andrews s.n.* (ILL). COLES: E. of Charleston, *Stover s.n.* (EI). COOK: Stoney Island, *A. Chase* 1996 (ILL). GALLATIN: One mile S. of Ridgway, *G. Dillard s.n.* (SIU). HENDERSON: Oquawka, *Patterson s.n.* (F). HENRY: N. of Penny Slough, *Dobbs* 9727 (ILLS). JACKSON: Between Crain & Grimsby, *Ahles* 5647 (ILL). KANE: Elgin, *Umbach s.n.* (ILL). KANKAKEE: Momence, collector unknown (ILL). LAWRENCE: NE. of Lawrenoeville, *Ahles* 4620 (ILL) MCHENRY: Algonquin, *Nason s.n.* (ILL). MACOUPIN: Carlinville, *Robertson* 9755 (ILLS). MASON: Six miles S. of Havana, *Rexroat* 3080 (ISM). MASSAC: Joppa, *Ahles* 6685 (ILL). MENARD: Athens, *Hall s.n.* (MO). OGLE: Oregon, *Moffatt s.n.* (ILL). PEORIA: Peoria, *McDonald s.n.* (ILL). PIKE: N. of Florence, *Evers* 21269 (ILLS). POPE: N. of Herod, *Ahles* 4684 (ILL). PULASKI: E. of Grand Chain, *Evers* 52503 (ILLS). PUTNAM: Lake Senachwine, *V. Chase* 10815 (ILL). RANDOLPH: Rock Castle Creek, *Bailey & Swayne* 1596 (SIU). ST. CLAIR: River shore, *H. Eggert s.n.* (MO). SANGAMON: Sangamon River, *Andrews s.n.* (ILL). TAZEWELL: Pekin, *V. Chase* 10851 (ILL). UNION: Union County State Forest, *Fuller* 797 (ILL). VERMILION: Kickapoo State Park, *Ahles* 3364 (ILL). WASHINGTON: Nashville, *French s.n.* (SIU). WINNEBAGO: Rockford, *E. Fell & G. Fell* 48-327 (ILL). WOODFORD: S. of Spring Bay, *V. Chase* 6213 (ILL).

11. CYPERUS SCHWEINITZII Torr. in Ann. Lyc. N. Y. 3:376. 1836. (Fig. 12).

Perennial with short rhizomes bearing corm-like swellings; culms 2-8 dm tall, usually scabrous, at least near the tip; leaves to 6 mm wide, seldom reaching the inflorescence, very scabrous along the margins, usually flat but occasionally revolute-margined; inflorescence with 1-2 oblong sessile spikes and 2-8 unequal rays over 8 cm long, with 3-6 scabrous-margined involucral bracts equalling or much exceeding the inflorescence; spikes ellipsoid to ovoid, with 5-15 very



Figs. 11 and 12. 11.—*Cyperus aristatus*. a. Spikelet, x 4. b. Achene, x 25. c. Scale, x 25. d. Map. 12.—*Cyperus schweinitzii*. a. Map. b. Achene, x 15. c. Scale, x 10. d. Spikelet, x 3.

ascending spikelets; spikelets flattened, 8- to 18-flowered, 12-25 mm long; scales ovate to rotund, with a mucro 0.5-1.5 mm long, with a scarious margin, 9- to 15-nerved, 2.5-4.0 mm long; rhachilla not winged; achenes trigonous, ellipsoid, 2.5-3.3 mm long, 1.0-1.2 mm broad, light brown.

Habitat.—Sandy soil.

Range.—Quebec to Idaho south to New Mexico, Illinois, northern Indiana, northern Ohio, and New Jersey.

Cyperus schweinitzii is most easily recognized by the mucro of the scales which is 0.5-1.5 mm long, the large achene (2.5-3.3 mm long), and the ascending spikelets. It is confused frequently with *C. filiculmis* var. *filiculmis.*

Specimens Examined: CASS: S. of Chandlerville, *Ahles* 2955 (ILL). CHAMPAIGN: E. of Urbana, *Buser* 1448 (ILL). COOK: Chicago, *Babcock* 3058 (ILL). HANCOCK: E. of Warsaw, *Evers* 38283 (ILLS). HENDERSON: Oquawka, *V. Chase* 5091 (ILL). HENRY: Four miles S. of Hooppole, *Dobbs* 9767 (ILLS). JACKSON: Along Gulf, Mobile, and Ohio Railroad, Murphysboro, *Mohlenbrock* 4514 (ILL). JO DAVIESS: Sandy banks of the Mississippi River, *Gleason & Gates* 2656 (ILL). KANKAKEE: SE. of Custer Park, *Steyermark* 64878 (F). LAKE: E. of Zion, *Brown* 165 (ILL). MCHENRY: Ringwood, *Vasey s.n.* (F). MASON: Havana, *Gleason s.n.* (ILL). MERCER: SE. of Keithsburg, *Evers* 48005 (ILLS). MORGAN: S. of Meredosia, *Evers* 41082 (ILLS). ROCK ISLAND: N. of Cordova, *Evers* 35466 (ILLS). SCOTT: N. of Bluffs, *Evers* 41066 (ILLS). STARK: N. of Duncan, *V. Chase* 793 (ILL). TAZEWELL: Near East Peoria, *V. Chase* 10770 (ILL). WHITESIDE: NW. of Erie, *Evers* 47618 (ILLS). WINNEBAGO: Rockford, *E. Fell & G. Fell* 48-341 (ILL). WOODFORD: Spring Bay, *V. Chase* 10002 (ILL).

12. CYPERUS HOUGHTONII Torr. Ann. Lyc. N. Y. 3:277. 1836. (Fig. 13).

Perennial with short rhizomes bearing corm-like swellings; culms 2-8 dm tall, smooth or nearly so; leaves to 4 mm wide, seldom reaching the inflorescence, usually with very smooth margins; inflorescence with 1 or 2 sessile spikes and 2-5 rays, with 2-5 usually smooth involucral bracts; spikes hemispherical, with ascending spikelets; spikelets flattened, 4- to 14-flowered, 5-22 mm long; scales rotund, obtuse and with a mucro, 11- to 15-nerved, 2.0-2.5 mm long, 1.0-1.5 mm broad; achenes trigonous, rounded below, nearly truncate above, 1.2-1.8 mm long, 0.8-1.2 mm broad, dark brown.

Habitat.—Sandy soil.

Range.—Quebec to Minnesota south to Iowa, northern Illinois, northern Indiana, and Virginia.

This species resembles *C. schweinitzii* but differs in its smaller achenes and its scales with only minute mucros. It differs from *C. filiculmis* var. *filiculmis* by its much broader achenes and scales.

C. houghtonii has been reported from Illinois by numerous authors, but almost all collections labelled as such in herbaria are actually either *C. schweinitzii* or *C. filiculmis* var. *filiculmis.*

Hunt s.n., which is probably adventive in Cook County, is the only

specimen seen during this study which can be referred to *C. houghtonii.* The natural range of this species probably should include Illinois, however.

Specimens Examined: **COOK: South side of Chicago, *Hunt s.n.* (ILLS).**

13. CYPERUS FILICULMIS Vahl, Enum. Pl. 2:328. 1806. (Fig. 14).

Perennial from hard corm-like rhizomes; culms very slender and wiry to somewhat more robust, to 8 dm tall, glabrous or slightly scabrous beneath the inflorescence; leaves flat or conduplicate, 1.0-5.5 mm wide, glabrous or with scabrous margins; inflorescence of a single sessile glomerule and sometimes with 1-several rays to 10 cm long, with up to 6 involucral bracts, some or all of which surpass the inflorescence; spikes hemispherical, but never completely spherical, with numerous radiating spikelets; spikelets 3- to 15-flowered, 3-20 mm long, with somewhat loose scales; scales acute or subacute, subcoriaceous, with hyaline margins, 5- to 9-nerved, 1.6-3.5 mm long; rhachilla wingless; style 3-cleft; achene trigonous, 1.3-2.0 (-2.2) mm long, 0.6-1.0 mm broad, black.

Two varieties occur in Illinois:

a. Plants with a central sessile glomerule and with 3-6 (-8) well-developed rays; spikelets (4-) 5- to 15-flowered; scales 2.4-3.5 mm long, some of the tips with a mucro 0.1-0.4 mm long; leaves 1.8-5.5 mm wide; achenes (1.7-) 1.8-2.2 mm long ....13a. *C. filiculmis* var. *filiculmis*

a. Plants with only a central sessile glomerule or occasionally with 1-2 rays; spikelets 3- to 8-flowered; scales 1.6-2.8 (-3.1) mm long, the tips acute or with a mucro less than 0.1 mm long; leaves 1.0-2.5 (-3.6) mm wide; achenes 1.2-1.8 (-2.0) mm long ....13b. *C. filiculmis* var. *macilentus*

13a. *Cyperus filiculmis* var. *filiculmis.*

Cyperus bushii Britton Man. Fl. North. U.S. 1044. 1901.

Cyperus mesochoreus Geise Am. Midl. Nat. 15:241-291. 1934.

Cyperus houghtonii Torr. var. *bushii* (Britton) Kükenth. *in* Kükenth., Pflanzenr. 20:469. 1936.

Cyperus houghtonii Torr. var. *uberior* Kükenth. *in* Kükenth., Pflanzenr. 20:469. 1936.

Much variation occurs among specimens of *Cyperus filiculmis.* The two varieties recognized in this study tend to intergrade with each other, but a general over-all largeness of *C. filiculmis* var. *filiculmis* separates the two.

Various specimens considered to be hybrids between *C. filiculmis* and *C. schweinitzii,* called *C. mesochoreus,* or perhaps between *C. filiculmis* and *C. houghtonii,* called *C. houghtonii* var. *uberior,* seem best treated as *C. filiculmis* var. *filiculmis.* These specimens have 7-15 flowers per spikelet, achenes 1.9-2.2 mm long, and usually some scabrosity on the culms beneath the inflorescence.

Confusion has arisen between *C. filiculmis* var. *filiculmis* and *C. schweinitzii.* The following table compares and contrasts some of the diagnostic characters:

	C. filiculmis var. *filiculmis*	*C. schweinitzii*
Mucro of scale	absent to 0.4 mm long	0.5-1.5 mm long
Culm	glabrous to moderately scabrous	harshly scabrous
Achene length	1.7-2.2 mm	2.5-3.3 mm
Spikelets	some ascending, some spreading, forming a hemispherical spike	all strongly ascending

Habitat.—Rocky or sandy soil.

Range.—Massachusetts to Michigan south to Nebraska, Texas, and Florida.

Specimens Examined: BOND: E. of Reno, *Evers* 18751 (ILLS). CASS: E. of Beardstown, *V. Chase* 11327 (ILL). CHAMPAIGN: Champaign, *Ahles* 6516 (ILL). COOK: Hyde Park, Chicago, *A. Chase* 1162 (ILL). HANCOCK: E. of Warsaw, *Evers* 38282 (ILLS). HENDERSON: W. of Lomax, *Evers* 18353 (ILLS). HENRY: *Dobbs* 17874a (ILLS). IROQUOIS: Five miles N. of Watseka, *Winterringer* 7050 (ISM). JO DAVIESS: SE. of East Dubuque, *Evers* 47490 (ILLS). KANKAKEE: Near St. Anne, *Jones* 16621 (ILL). LAKE: Three miles N. of Waukegan, *Fuller* 9031 (ISM). LEE: SE. of Amboy, *Evers* 49230 (ILLS). MCDONOUGH: *Myers* 111 (WI). MADISON: Wood River, *Evers* 38886 (ILLS). MARSHALL: Two miles N. of Lacon, *Evers* 39522 (ILLS). MASON: W. of Easton, *Evers* 47031 (ILLS). MENARD: SE. of Petersburg, *Evers* 45284 (ILLS). MERCER: SE. of Keithsburg, *Evers* 48011 (ILLS). OGLE: E. of Oregon, *Evers* 19370 (ILLS). ROCK ISLAND: Three miles NW. of Port Byron, *E. & G. Fell* F47-219 (ISM). SCHUYLER: S. of Browning, *Rexroat* 3090 (ISM). SCOTT: N. of Bluffs, *Evers* 41065 (ILLS). TAZEWELL: Pekin, *V. Chase* 10838 (ILL). WHITESIDE: N. of Fulton, *Ahles* 4243 (ILL). WILL: SE. of Wilmington, *Evers* 25568 (ILLS). WINNEBAGO: S. of Harrison Avenue, Rockford, *E. Fell* F48-348 (ISM). WOODFORD: S. of Spring Bay, *V. Chase* 10000 (ILL).

13b. *Cyperus filiculmis* var. *macilentus* Fern. Rhodora 8:128. 1906.

Cyperus macilentus Bickn. Bull. Torr. Club 35:478. 1908.

This slender phase of *C. filiculmis* more properly fits the epithet *filiculmis* than does the typical variety. In its most extreme form, the inflorescence of var. *macilentus* is reduced to a single sessile spike, the leaves are 1.1-1.4 mm wide, the scales 2.0-2.6 mm long, the achene 1.3-1.6 mm long, and the spikelets 3- to 6-flowered.

Some difficulty in distinguishing the two varieties is due in part to the fact that immature specimens of var. *filiculmis* strongly resemble mature var. *macilentus*. There is no doubt, however, that the two varieties intergrade considerably.

Habitat.—Sandy soil.

Range.—Similar to var. *filiculmis*, perhaps reaching somewhat farther south.

Specimens Examined: ADAMS: Quincy, *Evers* 906 (ILL). BOONE: W. of Belvidere, *E. Fell* 52655 (ISM). BUREAU: *Pepoon & Barrett* 6104 (ILLS). CALHOUN: NW. of Belleview, *Evers* 27247 (ILLS). CASS: Beardstown, *V. Chase*

11343 (ILL). CHAMPAIGN: Champaign, *Ahles* 6292 (ILL). CHRISTIAN: Taylorville, *Andrews s.n.* (ILL). COOK: Chicago, *A. Chase* 1188 (ILL). FULTON: Canton, *collector unknown* (ILL). GALLATIN: S. of Kedron, *Evers* 26777 (ILLS). HARDIN: E. of Lamb, *Evers* 45055 (ILLS). HENDERSON: N. of Oquawka, *Evers* 39754 (ILLS). HENRY: Dobbs 12875 (ILLS). IROQUOIS: N. of Donovan, *Ahles* 6878 (ILL). JACKSON: Ten miles NW. of Murphysboro, *Bailey & Swayne* 1512 (SIU). JERSEY: Pere Marquette State Park, *Fuller s.n.* (ISM). JO DAVIESS: S. of Hanover, *Steyermark* 40804a (ILL). JOHNSON: Near Buncombe, *Buser s.n.* (ILLS). KANE: Elgin, *Sherff* 1942 (ILL). KANKAKEE: Rock Creek, *Jones* 15879 (ILL). LAKE: Illinois Beach State Park, *Brown* 210 (ILL). LASALLE: Starved Rock State Park, *V. Chase* 10157 (ILL). LAWRENCE: E. of Billet, *Evers* 34720 (ILLS). LEE: Six miles NW. of Franklin Grove, *Keithley* 252 (ISM). MCDONOUGH: Pleasant Valley, *Myers* 568 (SIU). MCHENRY: Ringwood, *Vasey s.n.* (ILL). MADISON: Wood River, *Evers* 38885 (ILLS). MARSHALL: Two miles N. of Lacon, *Evers* 39509 (ILLS). MASON: E. of Havana, *V. Chase* 4016 (ILL). MENARD: S.E. of Petersburg, *Evers* 45274 (ILLS). MONROE: S. of Fults, *Bailey & Swayne s.n.* (ISM). MORGAN: N. of Meredosia, *Rexroat* 2070 (ISM). OGLE: Near Castle Rock, *Fuller* 10916 (ISM). PEORIA: Peoria, *V. Chase* 4530 (ILL). PIKE: Three miles S. of Kinderhook, *Evers* 24725 (ILLS). PUTNAM: S.E. of Putnam, *V. Chase* 16870 (ILL). RANDOLPH: E. of Marissa, *Bailey & Swayne s.n.* (SIU). ROCK ISLAND: NW. of Port Byron, *E. & G. Fell s.n.* (ISM). ST. CLAIR: Near Dupo, *Neill* 926 (ISM). SANGAMON: Clear Lake, *Fuller* 5657 (ISM). SCHUYLER: *Rexroat* 1711 (ISM). SCOTT: N. of Bluffs, *Evers* 24992 (ILLS). TAZEWELL: Pekin, *V. Chase* 12875 (ILL). WABASH: Palmyra, *Schneck s.n.* (ILL). WASHINGTON: One mile W. of Addieville, *Boewe* 17283 (ILLS). WHITE: NE. of Carmi, *Evers* 11242 (ILLS). WHITESIDE: N. of Fulton, *Ahles* 4241 (ILL). WILL: SE. of Wilmington, *Evers* 25560 (ILLS). WINNEBAGO: S. of Rockford, *Fuller* 2347-H (ISM). WOODFORD: Spring Bay, *V. Chase s.n.* (ILL).

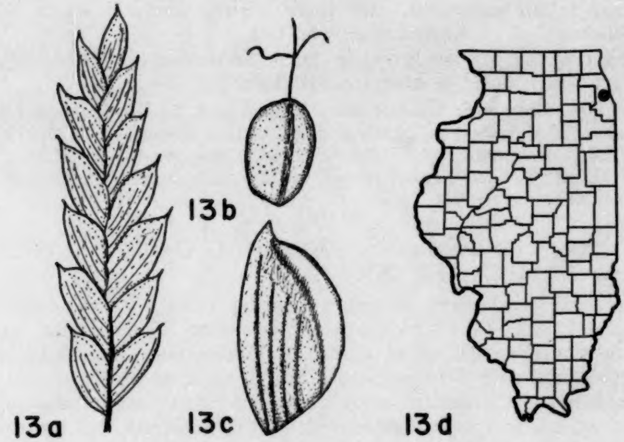
14. CYPERUS GRAYIOIDES Mohl. Brittonia 11:255-256. 1959. (Fig. 15).

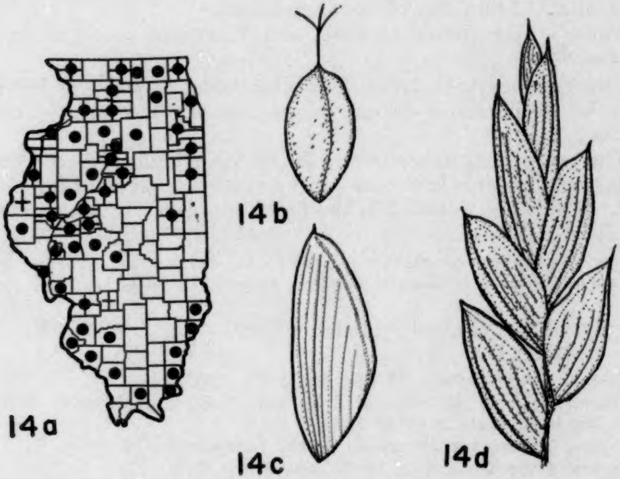
Perennial from a short horizontal rhizome; culms 30-60 cm tall, 0.7-1.2 mm broad, glabrous; leaves conduplicate, 2.0-3.5 mm wide, shorter than the culm, glabrous; inflorescence with 3-8 rays and 4-7 conduplicate bracts; spikes spherical, with numerous spikelets radiating in all directions; spikelets 4- to 7-flowered, to 10 mm long; scales loosely imbricate, somewhat remote, obtuse, the terminal scale acute, 9- to 13-nerved, 2.2-2.8 mm long; rhachilla wingless; stamens 3; styles 3-cleft; achene trigonous, oblongoid to broadly oblongloid, long apiculate, 2.0-2.6 mm long, black.

Habitat.—Sand prairies and blowouts.

Range.—Central and northwestern Illinois.

This species derives its name from the striking resemblance of it to the east coast *Cyperus grayii*. The two are similar in that the inflorescence is comprised of a sessile terminal head and usually five to several long peduncled heads which have the spikelets radiating in all directions. The unwinged rhachilla, the hyaline-margined scales, and the larger achenes separates this Illinois endemic from *C. grayii*. *Cyperus grayioides* resembles *C. filiculmis* on the basis of the hyaline





Figs 13 and 14. 13.—*Cyperus houghtonii.* a. Spikelet, x 3. b. Achene, x 10. c. Scale, x 15. d. Map. 14.—*Cyperus filiculmis.* a. Map: circle indicates var. *macilentus,* cross indicates var. *filiculmis.* b. Achene, x 10. c. Scale, x 15. d. Spikelet, x 4.

scales, but differs in that *C. grayioides* has larger achenes, spikelets radiating in all directions, and more loosely disposed scales. The resemblance to *C. schweinitzii* is even less.

This endemic species grows in pure sand along the Illinois River and in a sand prairie in northwestern Illinois.

Specimens Examined: MASON: Blow sand, August 22, 1954, *Rexroat* 1125 (holotype — ISM); Havana, bunch-grass association, August 13, 1903, *Gleason* 1047 (ILL). WHITESIDE: Sand prairie N. of Fulton, August 15, 1952, *Evers* 35442 (ILLS); blowout in sand prairie, N. of Fulton, August 15, 1952, *Evers* 35459 (ILLS).

15. CYPERUS LANCASTRIENSIS Porter ex A. Gray, Man. Bot., ed. 5:555. 1867. (Fig. 16).

Perennial with short rhizomes bearing one or more corm-like swellings; culms 3-60 cm tall, smooth; leaves to 10 mm broad, somewhat shorter than the culm, glabrous; inflorescence with 5-12 well-developed rays, with 6-10 involucral bracts, some of which surpass the rays; spikes short cylindric, with numerous horizontally radiating or reflexed spikelets; spikelets subulate, 3- to 6-flowered, 7-10 mm long; scales narrowly oblong, obtuse to subacute, closely appressed, 3.5-4.5 mm long, 7- to 13-nerved, yellowish; achenes trigonous, narrowly oblongoid, 2.0-2.6 mm long, 0.5-0.8 mm broad.

Habitat.—Moist and often sandy woods.

Range.—New Jersey to Ohio and Wisconsin south to Arkansas and Georgia.

In several ways, *C. lancastriensis* resembles *C. strigosus* but it can easily be distinguished by its longer achenes and usually reflexed spikelets.

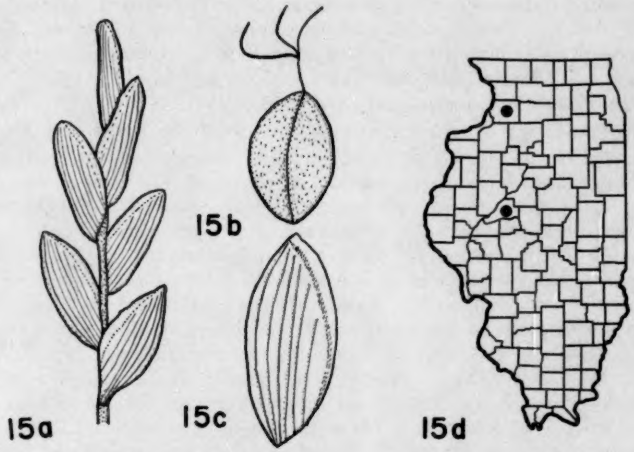
The range of *C. lancastriensis* in Illinois is limited to the extreme southern tip where it is very rare. It was not known from Illinois until 1949. Specimens recorded in the literature from Jackson County are actually *C. strigosus.*

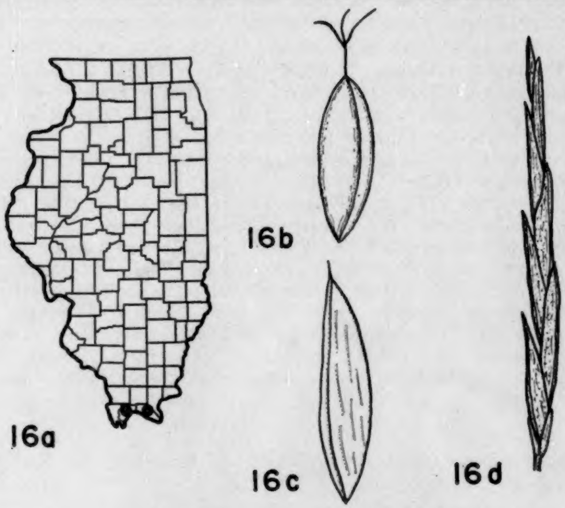
Specimens Examined: MASSAC: E. of Joppa, *Evers* 19952 (ILLS). PULASKI: One-half mile N. of Douglas Landing, *Evers* 5159 (ILLS).

16. CYPERUS OVULARIS (Michx.) Torr. Ann. Lyc. N. Y. 3:278. 1836. (Fig. 17).

Kyllinga ovularis Michx. Fl. Bor. Am. 1:29. 1803.
Cyperus ovularis var. *robustus* Britt. Bull. Torr. Club 13:214. 1886, *non* Boeckl. Linnaea 36:378. 1870.
Cyperus ovularis var. *sphaericus* Boeckl. Linnaea 36:378. 1870.
Cyperus wolfii Wood Bull. Torr. Club. 6:72. 1876.
Cyperus ovularis var. *wolfii* (Wood) Kükenth. Pflanzenr. 20:512. 1936.

Perennial from short rhizomes bearing corm-like swellings; culms smooth, 2.5-10.0 cm tall; leaves flat or rarely revolute, to 10 mm broad, much shorter than the culm, scabrous; inflorescence with a single sessile spike and usually 2-12 unequally ascending rays to 10 cm long, with 4-7 involucral bracts, the longest much exceeding the in-





Figs. 15 and 16. 15.—*Cyperus grayioides*. a. Spikelet, x 5. b. Achene, x 10. c. Scale, x 15. d. Map. 16.—*Cyperus lancastriensis*. a. Map. b. Achene, x 10. c. Scale, x 8. d. Spikelet, x 5.

florescence; spikes dense, globose, 8-20 mm in diameter; spikelets very numerous, radiating in all directions, 2- to 3-flowered, linear-lanceolate, 3-8 mm long; scales oblong, obtuse, 7- to 13-nerved, closely appressed, 3-4 mm long; achenes trigonous, oblongoid, apiculate, brown, 1.8-2.2 mm long, less than 1 mm broad.

Habitat.—Dry sandy woods, old fields.

Range.—New York to South Dakota south to Texas and Florida.

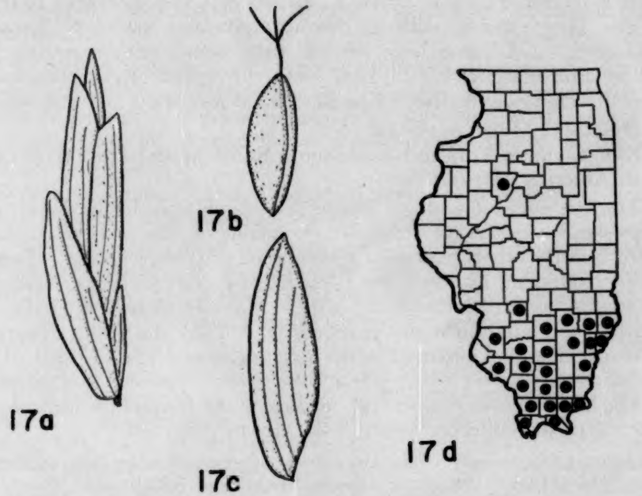
Cyperus ovularis is a most variable species. Numerous intergradient varieties and forms have been proposed, but lines of demarcation separating them are nonexistent. Var. *sphaericus* Boeckl. refers to specimens which, on the average, are smaller than the typical variety. At the other extreme exceedingly robust specimens have sometimes been segregated as var. *robustus* Britt. (*non* Boeckl.) or var. *wolfii* (Wood) Kükenth. Since all intergradations may be found from the smallest to the most robust specimens, it does not seem advisable to retain the varieties. Some Illinois material, notably *Mohlenbrock & Voigt* (Pope County) and *Mohlenbrock 10009* (Jackson County), requires a change in the range of certain characters over that given in current manuals. These specimens have up to 12 rays with spikes that measure 20 mm in diameter. One specimen from Jackson County, bearing merely a single sessile glomerule, resembles *C. filiculmis* var. *macilentus,* but differs in its very obtuse scales.

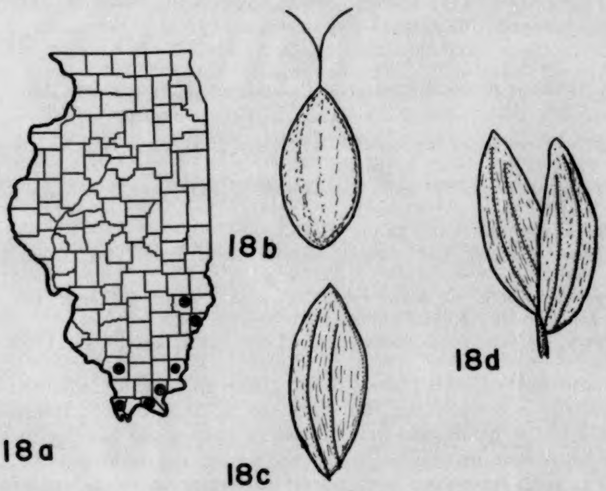
Specimens Examined: ALEXANDER: E. of Thebes, *Franklin* 13 (ILL). BOND: One mile N. of Waburn, *Evers* 39305 (ILLS). CLAY: S. of Flora, *Winterringer* 6052 (ISM). EDWARDS: N. of Albion, *Evers* 2019*i* (ILLS). FRANKLIN: N. of Benton, *Ahles* 5536 (ILL). GALLATIN: N. of Ridgway, *Evers* 34398 (ILLS). HARDIN: Six miles N. of Eichorn, *Ahles* 2753 (ILL). JACKSON: NW. of Makanda, *Cranwill s.n.* (ILL). JEFFERSON: S. of Mount Vernon, *Evers* 5494 (ILL). JOHNSON: Ozark, *Winterringer* 4061 (ISM). LAWRENCE: Lawrenceville, *Sivert s.n.* (ILL). MARION: Kell, *Burrill s.n.* (ILL). MASSAC: Metropolis, *Ahles* 2803 (ILL). MONROE: SE. of Poe, *Evers* 20506 (ILLS). PEORIA: Peoria, *Brendel s.n.* (ILL). PERRY: E. of Rice, *Evers* 12415 (ILLS). POPE: N. of Herod, *Winterringer* 5975 (ISM). RANDOLPH: Chester, *Winterringer* 3841 (ISM). RICHLAND: Olney, *Sherer* 621 (ILL). ST. CLAIR: Near French Village, *Fuller* 13143 (ISM). SALINE: SE. of Rudement, *Winterringer* 3515 (ISM). UNION: Between Ware and Wolf Lake, *Winterringer* 3458 (ISM). WABASH: Mt. Carmel, *Schneck s.n.* (ILL). WASHINGTON: N. of New Minden, *Winterringer* 3845 (ISM). WAYNE: E. of Geff, *Walker* 23 (ILL). WHITE: Norris City, *Ahles* 4677 (ILL). WILLIAMSON: Near Herrin, *Pepoon & Barrett s.n.* (ILLS).

17. CYPERUS DENSICAESPITOSUS Mattf. & Kükenth. *in* Kükenth., Pflanzenr. 20:597. 1936. (Fig. 18).

Kyllinga pumila Michx. Fl. Bor. Am. 1:28. 1803.
Kyllinga tenuifolia Steud. Syn. Pl. Cyp. 69. 1899.
Cyperus tenuifolius (Steud.) Dandy *in* Exell, Cat. Vasc. Pl. S. Tome 363. 1944, *non C. tenuifolius* Walp.

Sweet-smelling annual, cespitose, with fibrous roots; culms slender, 5-30 cm tall, smooth; leaves flat, soft, 1-3 mm wide, smooth, with the





Figs. 17 and 18. 17.—*Cyperus ovularis.* a. Spikelet, x 8. b. Achene, x 10. c. Scale, x 10. d. Map. 18.—*Cyperus densicaespitosus.* a. Map. b. Achene, x 25. c. Scale, x 20. d. Spikelet, x 20.

lower sheaths bladeless; inflorescence of 1 (-3) subglobose, sessile spikes 4-10 mm long and nearly as broad, with 2-4 spreading bracts to 10 cm long; spikes with numerous spikelets; spikelets 2-ranked, 1-flowered, 1.5-2.5 mm long; scales ovate, acute, with a distinct keel and hyaline margin, 1.5-2.2 mm long, the upper sterile; stamens 2; styles 2; achene lenticular, ellipsoid, 0.8-1.0 mm long, 0.5 mm wide.

Habitat.—Moist, open soil.

Range.—New York to Kansas south to Texas and Florida; Mexico; South America; Africa.

The presence of a single fertile flower per spikelet has been used by previous workers to separate the genus *Kyllinga* from *Cyperus.* There is little other reason to recommend this segregation. Fernald (1950), following Dandy (1944), calls this species *Cyperus tenuifolius,* but this is not the same entity which Walpole meant when he first used this combination many years earlier. Thus the epithet proposed by Mattfeld and Kükenthal is the first legitimate one applied to this species.

The fragrant odor given off by this plant frequently indicates its presence to the collector before it is actually observed.

Specimens Examined: ALEXANDER: Two and one-half miles NW. of Tamms, *Buser* 5374 (ILLS). GALLATIN: One-half mile S. of Ridgway, *G. Dillard s.n.* (SIU). JACKSON: Giant City State Park, *Mohlenbrock* 552 (SIU). MASSAC: E. of Joppa, *Evers* 19947 (ILLS). POPE: Bay bottoms, *Bailey & Swayne* 2875 (ILLS). WABASH: Mt. Carmel, *Patterson s.n.* (F).

18. CYPERUS FERRUGINESCENS Boeckl. in Linnaea 36:396. 1870. (Fig. 19).

Cyperus ferax sensu Pepoon 194. 1927, *non* L. C. Rich. Act. Soc. Hist. Nat. Paris 1:106. 1792, in part.

Cyperus michauxianus sensu Lapham 542. 1857, *non* Schult. *in* Roem. & Schult., Mant. 2:123. 1824.

Cyperus speciosus Vahl, Enum. 2:364. 1806.

Cyperus speciosus Vahl var. *squarrosus* Britt. Bull. Torr. Club 13:214. 1886.

Cyperus ferax L. C. Rich. subsp. *speciosus* (Vahl) Kükenth. var. *squarrosus* (Britt.) Kükenth. Pflanzenr. 20:620. 1936.

Cyperus odoratus sensu Gleason 251. 1952, *non* L. Sp. Pl. 46. 1753.

Coarse annual with fibrous roots; culms to 1 m tall, smooth; leaves flat, usually not equalling the culm, to 12 mm broad; inflorescence with 1-2 sessile heads and 2-12 simple or compound rays, with several of the numerous involucral bracts surpassing the inflorescence; spikes cylindric, with numerous horizontally radiating or ascending spikelets; spikelets flattened, 8- to 25-flowered, to 25 mm long with appressed or rarely loosely spreading scales; scales ovate, 1.7-3.0 mm long, with numerous faint nerves, reddish-brown or golden-brown, the terminal scale often subulate; rhachilla winged; achene obovoid-oblong, 1.0-1.7 mm long, red-brown or brown.

Habitat.—Rich moist soil.

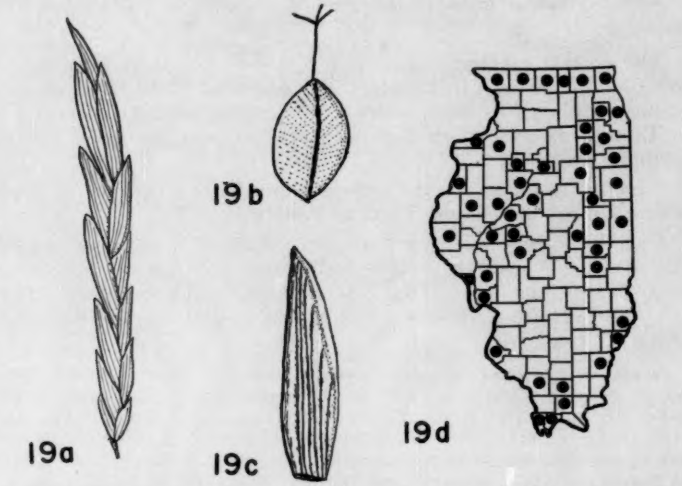
Range.—Massachusetts to Oregon south to California and Alabama.

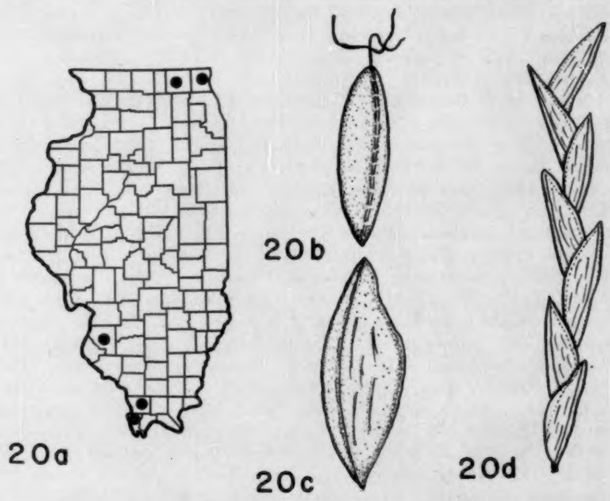
The correct nomenclature for this species has been in a state of confusion for years. If Linnaeus' *C. odoratus,* interpreted as being distinct because of its black achenes 1.5-2.0 mm long, is different from the Illinois material, than *Cyperus ferruginescens* Boeckl. is the first legitimate binomial.

Cyperus odoratus, in the restricted sense, is a species of southeastern United States and Tropical America.

Cyperus ferruginescens is a species subjected to frequent inundations which gives rise to peculiar individuals 1-20 cm tall with spikelets to 25 mm long and scales 2.5-3.0 mm long and very loosely spreading. The subulate terminal scales of this species help to distinguish it from *C. esculentus.*

Specimens Examined: ADAMS: Quincy, *Evers* 790 (ILL). BOONE: Belvidere, *E. Fell s.n.* (ISM). BROWN: E. of Cooperstown, *Evers* 40558 (ILLS). BUREAU: E. of Mineral, *Evers* 21211 (ILLS). CALHOUN: N. of Hardin, *Evers* 21417 (ILLS). CASS: S. of Beardstown, *Evers* 21390 (ILLS). CHAMPAIGN: Near Champaign, *Burrill & Sparrow* 14206½ (ILL). COLES: Lake Charleston, *Stover s.n.* (EI). COOK: South Chicago, *Sherff* 1766 (ILL). DOUGLAS: Villa Grove, *Evers* 52039 (ILLS). DUPAGE: Five miles S. of Downers Grove, *Evers* 32144 (ILLS). FORD: Paxton, *Moffatt* 509 (ILL). FULTON: Duck Island, *V. Chase* 4711 (ILL). GREENE: N. of Carrollton, *Winterringer* 12737 (ISM). GRUNDY: SW. of Gardner, *Evers* 21681 (ILLS). HANCOCK: S. of Nauvoo, *Evers* 20938 (ILLS). HENDERSON: N. of Oquawka, *Evers* 21013 (ILLS). HENRY: N. of Green River Station, *Dobbs* 9771 (ILLS). IROQUOIS: Gilman, *collector unknown* (ILL). JACKSON: Grand Tower, *Gleason s.n.* (ILL). JERSEY: Pere Marquette State Park, *Fuller* 542 (ISM). JO DAVIESS: S. of Blanding, *Evers* 36228 (ILLS). JOHNSON: E. of Vienna, *Evers* 32948 (ILLS). KANKAKEE: Wet grounds, *collector unknown* (ILL). KENDALL: NE. of Millington, *Evers* 40347 (ILLS). LAKE: Lake Villa, *Graham* 9419 (ISM). LAWRENCE: Lawrenceville, *Winterringer* 6963 (ISM). LIVINGSTON: One mile W. of Pontiac, *Fuller* 9170 (ISM). MCDONOUGH: N. of Bushnell, *Myers* 1170a (ISM). MCHENRY: Ringwood, *Vasey s.n.* (ILL). MCLEAN: Locality unknown, *Fuller* 299 (ISM). MARSHALL: S. of Sparland, *Evers* 19532 (ILLS). MASON: Cuba Island, *Anderson & Hawkins* 9773 (ILLS). MENARD: Athens, *Hall s.n.* (F). MONROE: S. of Fults, *Bailey & Swayne* 2806 (SIU). PEORIA: Peoria, *McDonald* 61 (ILL). PIATT: Monticello, *Seymour s.n.* (ILL). PULASKI: E. of Grand Chain, *Evers* 52506 (ILLS). ROCK ISLAND: Osburn, *Seymour s.n.* (ILL). SANGAMON: Curran, *Fuller* 6748 (ISM). SCHUYLER: SW. of Frederick, *Evers* 40507 (ILLS). SCOTT: W. of Winchester, *Evers* 20246 (ILLS). STARK: Near Wady Petra, *V. Chase* 784 (ILL). STEPHENSON: Near Freeport, *Serb* 9791 (ISM). TAZEWELL: Near East Peoria, *V. Chase* 3300 (ILL). VERMILION: Vermilion River, *G. Jones* 16244 (ILL). WABASH: Palmyra, *Schneck s.n.* (ILL). WHITE: Five miles E. of Crossville, *Winterringer* 6925 (ISM). WILL: Near Braidwood, *Graham* 9932 (ISM). WILLIAMSON: Carterville strip mine, *Bell s.n.* (SIU). WINNEBAGO: Rockford, *Fuller & Haime* 6F (ISM).





Figs. 19 and 20. 19.—*Cyperus ferruginescens*. a. Spikelet, x 3. b. Achene, x 15. c. Scale, x 15. d. Map. 20.—*Cyperus engelmannii*. a. Map. b. Achene, x 15. c. Scale, x 15. d. Spikelet, x 5.

19. CYPERUS ENGELMANNII Steud. Syn. Pl. Cyp. 47. 1855. (Fig. 20).

Cyperus ferax L. C. Rich. subsp. *engelmanni* (Steud.) Kükenth. Pflanzenr. 20:620. 1936.

Rather coarse annual with fibrous roots; culms to 60 cm tall, smooth; leaves to 6 mm wide, usually exceeding the culm, smooth; inflorescence of 1-several sessile spikes and 1-5 rays, with up to 6 involucral bracts much surpassing the inflorescence; spikes ellipsoid to oblongoid, with numerous horizontally radiating or ascending spikelets; spikelets terete, slender, to 18-flowered, 10-20 mm long, the flowers remote; scales brown, or reddish, ovate-lanceolate, acute, 2.2-3.0 mm long, with 7-13 rather faint nerves, the tip of one barely reaching the base of the one above it on the same side, thereby giving the spikelet a rather zigzag appearance; rhachilla winged; achenes linear-oblong, 1.5-2.2 mm long.

Habitat.—Wet ground.

Range.—Massachusetts and Minnesota south to Nebraska and Virginia.

Kükenthal (1936) maintains that this is nothing more than a sparsely-flowered variety of *Cyperus ferax*. The uniquely peculiar arrangement of the scales, however, seems to indicate the necessity for separating *C. engelmannii* as a distinct species.

Several Illinois collections previously referred to this are actually *C. ferruginescens*. Only a very few stations are known for *C. engelmannii* in Illinois, where it must be considered exceedingly rare. The type locality, usually attributed to St. Louis, Missouri, is actually based on an Engelmann collection along Cahokia Creek opposite St. Louis in St. Clair County, Illinois.

Specimens Examined: ALEXANDER: Horseshoe Lake S. of Olive Branch, *Evers* 41483 (ILLS). LAKE: Cedar Lake, *Gleason & Shobe* 153 (ILL). MCHENRY: Ringwood, *Vasey s.n.* (F). ST. CLAIR: Cahokia Creek, *Engelmann s.n.* (MO). UNION: S. of Ware, along Route 146, *Pepoon & Barrett s.n.* (ILLS).

REFERENCES

BOECKELER, OTTO 1868. Die Cyperaceen des Königlichen Herbarium zu Berlin. *Linnaea*, **35**:297-612.

———1870. Die Cyperaceen des Königlichen Herbarium zu Berlin. *Linnaea*, **36**:271-410.

BRITTON, NATHANIEL L. 1886. A preliminary list of North American species of *Cyperus*, with descriptions of new forms. *Bull. Torrey Club*, **13**:205-216.

CLARKE, C. B. 1883. *Cyperus. Journ. Linn. Soc.*, **20**:237-304.

———1884. On the Indian Species of *Cyperus*. *Ibid.*, **21**:1-202.

FERNALD, MERRITT L. 1950. *Gray's Manual of Botany*. The American Book Company, New York. 632 pp.

GAERTNER, JOSEPH 1788. *De fructibus et seminibus plantarum*. **1**:12.

GLEASON, HENRY A. 1952. *The New Britton and Brown Illustrated Flora of the Northeastern United States*. The New York Botanical Garden, New York. Vol. **1**:246-258.

JONES, G. NEVILLE 1950. *Flora of Illinois.* The University Press, Notre Dame, Indiana. 370 pp.

KÜKENTHAL, GEORG. 1936. Cyperaceae-Scirpoideae-Cypereae. *Das Pflanzenr.,* **20**:1-671.

LINNAEUS, CAROLUS 1753. *Species Plantarum,* ed. I:44-47.

O'NEILL, HUGH 1942. Cyperaceae of North and South America. *Rhodora,* **44**:43-64, 77-89.

PLINY THE ELDER 77 A.D. *Historia Naturalis.* **21**:69.

ROTTBOELL, CHRISTEN F. 1773. *Descriptionum et Iconum rariores.* **6**:1-71.

TORREY, JOHN 1836. Monograph of the North American Cyperaceae. *Ann. Lyc. N.Y.,* **3**:339-451.

VAHL, MARTIN 1806. *Enumeratio Plantarum.* **2**:1-423.

ZINN, JOHANN G. 1757. *Catalogus plantarum horti academici et agri Gottingensis.*

A Synopsis of the Cave Beetles of the Genus Pseudanophthalmus of the Mitchell Plain in Southern Indiana (Coleoptera, Carabidae)

THOMAS C. BARR, JR.
Tennessee Polytechnic Institute, Cookeville

Thirteen species and subspecies of cave beetles of the genus *Pseudanophthalmus* Jeannel have been reported from the Mitchell Plain of southern Indiana. Horn (1871, 1883), Jeannel (1931, 1949), and Krekeler (1958) have described and illustrated the majority of these forms in considerable detail. The present paper is intended to be used in conjunction with the papers of Jeannel (1949) and Krekeler (1958), and no attempt has been made to repeat descriptions of forms which have been adequately treated by these authors. The discovery of a "lost" species in Wyandotte Cave and a nearby cavern necessitates a new combination and the changing of several trinomials. A new species, from Lawrence County, is described.

For reasons stated in an earlier paper (Barr, 1959) the writer has applied the polytypic species concept to the systematics of *Pseudanophthalmus* and other genera of troglobious carabids. An alternative taxonomic approach was offered by Krekeler (1958), who regarded each morphologically distinct cave population (or group of similar populations in closely associated caves) as genetically isolated.

The specimens upon which the present paper is based were collected in Crawford, Harrison, Lawrence, Monroe, Orange, Owen, and Washington Counties, Indiana, during the summer of 1957 and the fall of 1958. Dr. Carl H. Krekeler, Valparaiso University, whose recent (1958) paper is the most important single contribution to our knowledge of Indiana anophthalmids, provided a topotype *P. morrisoni* and a paratype *P. youngi donaldsoni* for examination. One *P. morrisoni* and six *P. youngi donaldsoni* were collected for the writer by Mr. Thomas L. Poulson.

Deep appreciation is expressed to Mr. Lewis D. Lamon, Corydon, Indiana, and to Miss Leona Hert, Springville, Indiana, for assistance in collecting the material discussed below. Mr. Robert Louden, manager of Wyandotte Cave, was most courteous and helpful. Dr. Harold J. Grant, Academy of Natural Sciences of Philadelphia, kindly compared the writer's topotypes with Horn's types of *Anophthalmus eremita* and *A. tenuis*.

Five species groups and six species are recognized in the present study, four of the groups being monotypic. The species may be separated by the following key.

KEY TO KNOWN SPECIES OF PSEUDANOPHTHALMUS OF THE MITCHELL PLAIN IN SOUTHERN INDIANA

1 Posterior pronotal angles small or quadrangular, not projecting posterior to the base of the pronotum; median lobe of labrum not prominent.......... 2

1′ Posterior pronotal angles acute, produced backward beyond the base of the pronotum; medium lobe of labrum well defined, prominent................ 4

2 Size medium (3.8-4.9 mm) or large (5.3-5.4 mm); longitudinal elytral striation absent or very indistinct.. 3

2′ Size small (3.2-3.8 mm); longitudinal elytral striation shallow but distinct (Lawrence County) .... *P. leonae* n. sp.

3 Size medium (3.8-4.9 mm); longitudinal striation of elytra present but indistinct (Lawrence County) .... *P. emersoni* Krekeler

3′ Size large (5.3-5.4 mm); longitudinal striation of elytra completely absent, disc strongly alutaceous (Crawford and Harrison Counties).. *P. eremita* (Horn)

4 Right copulatory piece a broad, curved membrane, concave dorsally when seen in lateral view (Fig. 1); left piece a rolled, membranous rod; recurved portion of apical stria usually (but not always) running into the third longitudinal stria (Crawford, Harrison, Lawrence, Orange, Washington Counties).. *P. tenuis* (Horn) new comb.

4′ Transfer apparatus not as described above; recurved portion of apical stria usually (but not always) directed toward the fifth longitudinal stria 5

5 Transfer apparatus a tube, the left dorsal piece half the size of the right ventral piece; apex of right ventral piece projecting beyond the left dorsal, shaped like the bow of a canoe (Fig. 2) (Washington and Lawrence Counties) .... *P. youngi* Krekeler

5′ Transfer apparatus of two sinistrally concave, spatulate copulatory pieces (Fig. 3) which form a spout, the left dorsal piece smaller and nested within the right ventral piece (Lawrence, Monroe, and Owen Counties) .... *P. shilohensis* Krekeler

EREMITA GROUP

Pseudanophthalmus eremita (Horn)
Figs. 4, 7

Anophthalmus eremita Horn 1871: 325. Horn 1883: 272. Leng 1920: 55. Type: Wyandotte Cave, Crawford Co., Indiana (Acad. Nat. Sci. Philadelphia).

Not *Pseudanophthalmus eremita* of Jeannel 1928: 131. Jeannel 1931: 466. Valentine 1932: 275. Jeannel 1949: 56. Krekeler 1958: 170.

P. eremita (Horn) is known from only three specimens, all males: (1) the type, collected by E. D. Cope in Wyandotte Cave; (2) one specimen, Langdon's Cave, Harrison Co., Indiana (July 14, 1957, T.C.B.); and (3) one specimen, Wyandotte Cave (October 26, 1958, L. D. Lamon, L. D. Lamon, Jr., and T. C. B.). Female unknown.

Although Horn's descriptions (1871, 1883) of *eremita* and *tenuis* are explicit and adequate for differentiation of the two species, the rarity of the former apparently led to the supposition that only one

species inhabited Wyandotte Cave. *Anophthalmus tenuis* Horn was listed as a synonym of *A. eremita* by Leng (1920) and most later authors followed suit. The present author has avoided committing the same error purely through a happy circumstance — the discovery of both forms in Langdon's Cave, 2.4 miles SE. of Wyandotte, which induced him to conduct an extensive search for beetles in the type cave. A six-hour collecting trip yielded thirty specimens, twenty-nine of which were *tenuis* and one of which was *eremita*. A description of this specimen, a late teneral, follows.

Length 5.3 mm. Form robust and rather depressed. Color pale, yellow, testaceous. Head of moderate proportions (1.15 x 0.83 mm, index 0.72); labrum doubly emarginate, the median lobe low but well defined. Pronotum transverse (0.92 x 1.10 mm, index 1.20), subconvex, sparsely pubescent; greatest width at anterior setae, behind which the sides curve very gently back to the shallow basal sinus; posterior angles blunt, almost quadrangular. Elytra elongate-oval (2.85 x 1.84 mm, index 0.65), tapered apically, with a small cauda; surface wholly devoid of longitudinal striae, strongly alutaceous; rows of punctations faintly visible; pubescence sparse, locally arranged in longitudinal rows; humeri prominent, rounded, serrulate, setose; humeral set of setae closely spaced, resulting in a high chaetotaxial index (0.63); first discal seta posterior to fourth marginal puncture; apical recurrent stria broadly arcuate, turning abruptly and running to the third discal puncture. Aedeagus (Fig. 4) long and slender (1.19 mm); basal bulb very large and strongly flexed; basal keel absent; median lobe straight posterior to basal flexure; apex abruptly produced into a long, blunt spine on the left (dorsal, *in situ*) side, with a slight enlargement at the end; transfer apparatus of two elongate, rodlike copulatory pieces with blunt, rounded apices; left piece a little longer and narrower than right piece; internal sac armed with dense rows of small scales; parameres long, bearing four long, stout setae. Antennae of moderate length (3.54 mm, antennal index 0.66).

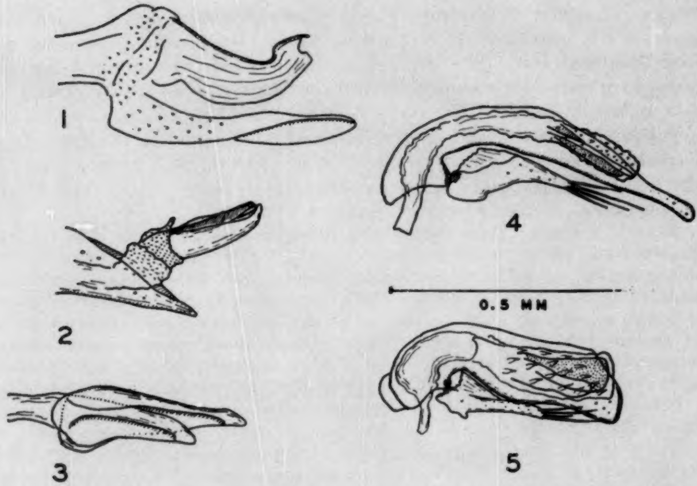
The specimen from Langdon's Cave (Fig. 7) differs in minor particulars: (1) it is fully sclerotized; (2) the elytra are not caudate; (3) the aedeagus bears a small basal keel and is slightly thicker in the middle portion, though of nearly the same length (1.17 mm). Like the topotype described above, the type male is caudate (H. J. Grant, pers. comm.). The writer has seen caudate elytra elsewhere in the genus only in a single *P. s. shilohensis* Krekeler.

Pseudanophthalmus emersoni Krekeler

Pseudanophthalmus emersoni Krekeler 1958: 176. Type: Donnehue's Cave, Lawrence Co., Indiana (Chicago Nat. Hist. Mus.).

P. emersoni is known only from the type locality (C. H. Krekeler and W. W. Bloom, 1950; C. H. Krekeler, 1953; T. C. B., 1957) where it coexists with *P. s. shilohensis*. It is apparently not very abundant.

With *eremita*, this species shares group characters — sparsely pubescent pronotum and elytra; trilobate labrum; transverse pronotum with quadrate hind angles; obsolescent elytral striation; and the nature of the apical recurrent stria and aedeagus. The position of the first discal stria is well behind the level of the fourth marginal puncture in both *eremita* and *emersoni*.



Figs. 1-5.—1. *Pseudanophthalmus t. tenuis* (Horn), King's Cave, Harrison Co., Indiana; transfer apparatus of male genitalia. Actual size, 0.30 x 0.14 mm. 2. *Pseudanophthalmus youngi donaldsoni* Krekeler, paratype, Donaldson's Cave complex, Lawrence Co., Indiana; transfer apparatus exserted from median lobe. Actual size, 0.57 x 0.14 mm. 3. *Pseudanophthalmus s. shilohensis* Krekeler, topotype, Shiloh Church Cave, Lawrence Co., Indiana; transfer apparatus, right dorsal and left ventral copulatory pieces slightly separated. Actual size, 0.29 x 0.14 mm. 4. *Pseudanophthalmus eremita* (Horn), topotype, Wyandotte Cave, Crawford Co., Indiana; aedeagus. 5. *Pseudanophthalmus leonae* n. sp., holotype male, Hert Hollow Cave, Lawrence Co., Indiana; aedeagus. (Scale of 0.5 mm for Figs. 4 and 5).

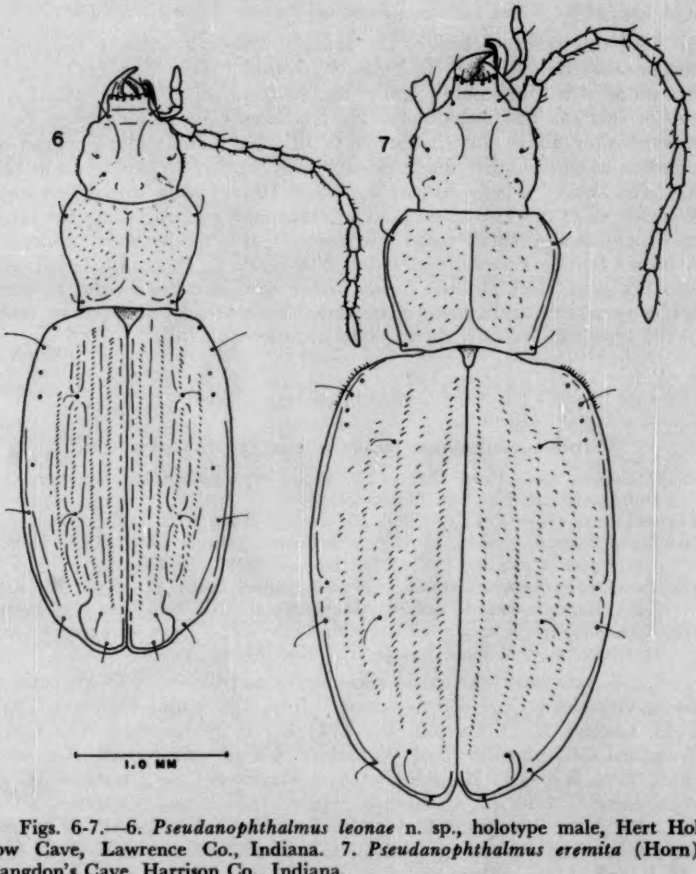
LEONAE GROUP

Size very small (3.2-3.8 mm). Head short and rounded, labrum trilobate. Pronotum transverse, pubescent, posterior angles quadrangular. Elytra oblong-oval, pubescent; humeri setose but not serrulate; first discal seta at level of fourth marginal puncture; chaetotaxial index high (0.67-0.68); apical recurrent stria rounded, bending sharply to the third longitudinal stria at the level of the third discal puncture. Aedeagus short and thick, basal flexure almost a right angle, apex blunt and truncate; basal keel small, subterminal; right copulatory piece large and broad (membranous?) in lateral view, triangular, apex hatchet-shaped; left piece narrower, a blunt rod (hollow or rolled?); internal sac armed with oblique rows of large scales; genital index 0.13. Type: *P. leonae* new species.

Pseudanophthalmus leonae new species.
Figs. 5, 6

Length 3.18-3.80, mean 3.58 mm. Color pale, rufo-testaceous.

Form robust and depressed. Head small and rounded; labrum doubly emarginate, the median lobe quite low but distinct. Pronotum transverse (index 1.19-1.23, mean 1.20), pubescent; anterior angles blunt; sides arcuate, basal sinus beginning about the basal third; posterior angles small, quadrangular; base very slightly concave to irregular. Elytra elongate-oval, depressed; disc with rows of pubescence; longitudinal striae very shallow but distinct, somewhat indented at punctures of first and second discal setae; first discal seta a little posterior to the level of the fourth marginal papilla; humeri rounded, setose but not serrulate; prehumeral border medium oblique to the midline; apical recurrent stria a wide arc running abruptly at its interior ter-



Figs. 6-7.—6. *Pseudanophthalmus leonae* n. sp., holotype male, Hert Hollow Cave, Lawrence Co., Indiana. 7. *Pseudanophthalmus eremita* (Horn), Langdon's Cave, Harrison Co., Indiana.

minus into the third longitudinal stria, in some specimens continuing to the second stria. Antennae scarcely reaching the middle of the elytra when laid back. Legs rather long. Aedeagus 0.51 mm long, small, short, and thick; transfer apparatus large (0.27 the length of the median lobe), left piece about three-fourths as long as right piece; parameres slender, bearing four long setae of unequal length.

Type series. Holotype male, allotype female, and two paratypes, Hert Hollow Cave, two miles SW. of Springville, Lawrence Co., Indiana, August 18 and 19, 1957, Catherine K. Barr and T. C. B. Holotype and allotype deposited in the American Museum of Natural History.

Holotype. Total length 3.78 mm, head 0.83 x 0.69 mm, pronotum 0.74 x 0.87 mm, elytra 2.16 x 1.32 mm, antennae 2.01 mm, aedeagus 0.51 mm.

Allotype. Total length 3.18 mm, head 0.78 x 0.60 mm, pronotum 0.60 x 0.74 mm, elytra 1.75 x 1.15 mm, antennae 2.01.

This tiny beetle is one of the smallest known species in the genus, comparable in size to *P. lallemanti* Jeannel (West Virginia). By its size alone it is immediately distinguished from all other described species of Indiana anophthalmids. Hert Hollow Cave is located at Sycamore Valley Farm, on the property of Miss Leona Hert, whose assistance and hospitality made possible the capture of this unusual beetle. The "cave" is only 30 feet long, 8 to 10 feet wide, and 5 feet high. Wooden steps descend to a small subterranean stream, along the edges of which, among small rocks and rootlets, the beetles were collected. A larger female *Pseudanophthalmus,* assigned to *P. s. shilohensis,* was also taken in Hert Hollow Cave. Since the cave floods and is much colder in winter and spring, it is probable that *P. leonae* can be taken in the type locality only during late summer and fall.

TENUIS GROUP

Pseudanophthalmus tenuis tenuis (Horn) new comb.

Anophthalmus tenuis Horn 1871: 327. Type: Wyandotte Cave, Crawford Co., Indiana (Acad. Nat. Sci. Philadelphia).

Anophthalmus eremita, Leng 1920: 55. Not of Horn 1871: 325.

Pseudanophthalmus eremita of various authors. Jeannel 1928: 131. Jeannel 1931: 466. Valentine 1932: 275. Jeannel 1949: 56. Krekeler 1958: 170.

Syn. *Pseudanophthalmus eremita longicollis* Jeannel 1949: 57. Type: Bradford Cave, Harrison (not Crawford) Co., Indiana (Mus. Nat. Hist. Nat. Paris).

Syn. *Pseudanophthalmus bloomi* Krekeler 1958: 172. Type: Langdon's Cave, Harrison Co., Indiana (Chicago Nat. Hist. Mus.).

P. t. tenuis was collected in eight caves, as follows: (1) Wyandotte Cave, Crawford Co.—33 specimens (July, 1957, and October, 1958, L. D. Lamon, L. D. Lamon, Jr., T. C. B.). (2) Seibert's Well Cave, Crawford Co., ¼ mile S. of Wyandotte Cave—one female (October, 1958, T. C. B.). (3) Langdon's Cave, Harrison Co., 2.4 miles SE. of Wyandotte Cave — 7 specimens (July, 1957, and October, 1958, T. C. B.). (3) Langdon's Cave, Harrison Co., 2.4 miles SE. of Wyandotte Cave — 7 specimens (July, 1957, and October, 1958, T. C. B.). (4) King's Cave, Harrison Co., 3.5 miles SE. of Corydon — 18

specimens (July, 1957, T. C. B.). (5) Binkley's Cave, Harrison Co., one mile S. of Corydon—78 specimens (August, 1957, Catherine K. Barr, T. C. B.). (6) Bradford (Steerstetter) Cave, Harrison Co., 0.5 mile E. of Bradford on the left bank of Corn Creek—33 specimens (August, 1957, Leslie Hubricht and T. C. B.). This is the Bradford Cave described by A. S. Packard (1888) who wrote that anophthalmid beetles were more abundant here than in any other cave he had visited. (7) Sweet Potato Cave, Harrison Co., 0.6 mile N. of Byrneville on the right bank of Corn Creek—one male and two females (August, 1957, T. C. B.). (8) Goss Cave, Washington Co., two miles SW. of Martinsburg—17 specimens (August, 1957, L. D. Lamon and T. C. B.).

Variations in six populations of *P. t. tenuis* are presented in Table I. No consistent qualitative variations were discovered. The meristic data obtained indicate a modicum of local variation but do not justify subspecific differentiation from the Wyandotte population. "'Total length" was measured in millimeters, from the tips of the mandibles to the apices of the elytra. The "pronotal index" is the greatest width of the pronotum divided by the length measured along the midline. The "chaetotaxial index," as defined by Valentine (1945), is the dis-

TABLE I.—Meristic variations in different cave populations of *Pseudanophthalmus t. tenuis* (Horn)[1]

Cave	No. Specimens	Total Length	Pronotal Index	Chaetotaxial Index
Wyandotte	30	5.12 ± 0.06	1.07 ± 0.01	0.46 ± 0.01
Langdon's	7	4.90 ± 0.14	1.12 ± 0.03	0.46 ± 0.01
King's	18	5.00 ± 0.05	1.09 ± 0.01	0.49 ± 0.01
Binkley's	20	5.21 ± 0.02	1.07 ± 0.01	0.46 ± 0.01
Bradford	20	4.84 ± 0.06	1.11 ± 0.01	0.48 ± 0.01
Goss	17	5.02 ± 0.08	1.09 ± 0.01	0.46 ± 0.01

		No. Aedeagi	Aedeagus Length
Wyandotte	30	5	0.81 ± 0.02
Langdon's	7	4	0.83 ± 0.01
King's	18	5	0.83 ± 0.02
Binkley's	20	5	0.82 ± 0.01
Bradford	20	6	0.80 ± 0.01
Goss	17	5	0.83 ± 0.01

[1] All lengths in millimeters.

tance between the first and fourth marginal elytral punctures divided by the distance between the fourth and fifth punctures, and indicates the degree of spacing of the humeral set of four prominent setae.

The distinguishing characteristics of *longicollis* (Jeannel, 1949) were said to be (a) pronotum longer than wide, and (b) apex of aedeagus more attenuate. With a pronotal index which averages 1.11, the Bradford Cave population as a whole is quite different from what Jeannel's two cotypes led him to believe. Of the six aedeagi examined, two were slender and attenuate, but the other four were indistinguishable from typical Wyandotte *tenuis*.

In his diagnosis of *bloomi*, Krekeler (1958) lists four criteria for distinguishing *bloomi* from the Wyandotte population: (a) size smaller, (b) chaetotaxial index higher, (c) apical stria curved, not sinuate or parallel to the suture, and (d) left copulatory piece not subapically constricted and deflected. As indicated in Table I, the mean length of the writer's series from Wyandotte is 5.12 ± 0.06, whereas Krekeler's series averaged 5.32 ± 0.07, a difference probably attributable to sampling error. The average lengths of Krekeler's and the writer's series of beetles from Langdon's Cave are 4.80 ± 0.12 and 4.90 ± 0.14, respectively. Table I shows identical means (0.46 ± 0.01) for chaetotaxial indices in the writer's samples from both caves. The apical recurrent stria appears singularly unreliable in both Wyandotte and Langdon's populations. In the writer's seven Langdon's specimens the recurrent portion of the stria may be (a) arcuate, with three variations; (b) subparallel to the suture; (c) flared laterally to connect with the 5th longitudinal stria; or (d) weakly sinuate. Similar variations obtain among Wyandotte beetles.

The structure of the *tenuis* transfer apparatus has proved difficult to interpret in whole mounts of aedeagi. Jeannel (1931) confused the right and left pieces, and as he himself admitted, his earlier representation of this structure (1928) was wholly inaccurate. In *tenuis, shilohensis,* and *youngi* the writer found it necessary to dissect the transfer apparatus from the median lobe in order to determine its structure. In the following description of the *tenuis* apparatus (Fig. 1) both Krekeler (pers. comm., April 2, 1959) and the writer are essentially in agreement.

The right piece, a large membrane supported at the base by a sclerotized thickening, is flexible and varies slightly in length in any preparation. It is medially concave and partially envelops the left piece; in lateral view it appears dorsally concave. The apex bears a fine, irregular hook dorsally, with a notch below. The left piece is a rolled half tube, open medially along its length, with thickened walls and spiny armature. It has the shape of a tall cone, tapering apically and terminating in an ellipsoidal, translucent plate. The "normal" position of this terminal plate is presumably vertical, but in the preparation of slides it may rotate as much as 120°, varying in appearance with the angle at which it is viewed. In the examination of about 35 aedeagi of *tenuis,* no left piece was encountered which was

constricted subapically, though the variable degree of rotation presents several aspects in lateral view.

The known range of *P. t. tenuis* is roughly triangular, about twelve miles broad at the base and about eighteen miles along each of the other two sides. This beetle is thus an abundant, highly variable, wide-ranging form similar in distribution and variation to *P. menetriesi* (Motschulsky) and *P. r. robustus* Valentine (Kentucky and Tennessee species, respectively). Additional collecting, especially in southwestern Harrison County, may possibly increase the number of localities for this subspecies.

Pseudanophthalmus tenuis stricticollis Jeannel

Pseudanophthalmus eremita stricticollis Jeannel 1931:45. Type: Marengo Cave, Crawford Co., Indiana (Mus. Nat. Hist. Nat. Paris).
Pseudanophthalmus stricticollis, Krekeler 1958:170.

This subspecies is known only from Marengo Cave, twelve miles N. of Wyandotte Cave (C. Bolivar, R. Jeannel, H. Morrison, 1928; C. H. Krekeler, 1950; L. D. Lamon, Catherine K. Barr, T. C. B., 1957). The longer antennae, larger size, lower chaetotaxial index, and larger aedeagus easily distinguish *stricticollis* from nominate *tenuis* (cf. Jeannel, 1931; Krekeler, 1958).

Pseudanophthalmus tenuis jeanneli Krekeler

Pseudanophthalmus jeanneli Krekeler 1958:171. Type: Elrods Cave, Orange Co., Indiana (Chicago Nat. Hist. Mus.).

P. t. jeanneli is known only from five specimens taken in Elrod's Cave, which opens at the edge of Wesley Chapel Gulf (C. H. Krekeler and W. W. Bloom, 1950; Catherine K. Barr, T. C. B., 1957). The average length for the five specimens is 5.34 ± 0.21 mm, the pronotal and chaetotaxial indices for four are 1.09 ± 0.06 and 0.46 ± 0.03, respectively, and the three aedeagi measure 0.88, 0.94, and 0.96 mm. This subspecies may be distinguished from most of the other subspecies of *tenuis* by its larger aedeagus and longer antennae (index 0.65-0.71, av. 0.67), and from *stricticollis* by the shorter recurved portion of the apical stria.

Pseudanophthalmus tenuis morrisoni Jeannel

Pseudanophthalmus eremita Morrisoni Jeannel 1931:451. Valentine 1932: 275. Jeannel 1949:56. Type: Donaldson Cave, Lawrence Co., Indiana (Mus. Nat. Hist. Nat. Paris).
Pseudanophthalmus morrisoni, Krekeler, 1958:171.

This subspecies is readily distinguished by its larger size, greater aedeagal length, and the unusually wide pronotum. It is known only from the Donaldson Cave complex in Spring Mill State Park (R. Jeannel, C. Bolívar, H. Morrison, 1928; C. H. Krekeler, 1950; T. L. Poulson, 1957; T. C. B., 1957).

Pseudanophthalmus tenuis blatchleyi new subspecies
Fig. 8

Type. A unique male from Truitt's Cave, near Bloomington, Monroe Co., Indiana, U. S. National Museum, acquired as part of the Wickham collection. Collection data other than locality unknown. Female unknown.

Length 5.90 mm. Head unusually wide (1.29 x 1.01 mm, index 0.79). Pronotum normal (1.10 x 1.19 mm, index 1.08), posterior angles a little smaller and less produced. Elytra 3.26 x 1.93 mm, index 0.59; chaetotaxial index 0.42; apical recurrent stria short and rounded on left elytron, turning somewhat abruptly inward at its anterior terminus on the right elytron, running into third longitudinal stria. Antenna 4.02 mm, index 0.68. Aedeagus (Fig. 8) 1.03 mm, large and thick, apex somewhat truncate; copulatory pieces subequal in length; parameres bearing five setae.

P. t. blatchleyi is distinguished from most subspecies of *tenuis* by its greater total length and aedeagal length. From *morrisoni* — a subspecies comparable in both of these characters — it differs in the narrower pronotum and larger, wider head. From *P. shilohensis mayfieldensis,* which inhabits the same cave, it is readily distinguished by the larger size, wider head, less sharply defined median lobe of the labrum, reduced hind angles of the pronotum, apical recurrent stria running to the third and not to the fifth longitudinal elytral stria, and the transfer apparatus.

This subspecies is unfortunately known only from the type. During removal of the aedeagus the apex of the median lobe was accidentally broken off, and the accompanying drawing (Fig. 8) is consequently a reconstruction from the two pieces. This circumstance, however, afforded an excellent view of the transfer apparatus. It is to be hoped that future collections will yield additional specimens and permit an adequate description of the range of variation in *blatchleyi.* The writer is not completely satisfied that *morrisoni* and *blatchleyi* contribute to the same gene pool as *tenuis* s. str., *stricticollis,* and *jeanneli,* but would prefer to have more evidence of genetic isolation before elevating them to full species.

This subspecies is named in honor of W. S. Blatchley, a pioneer in

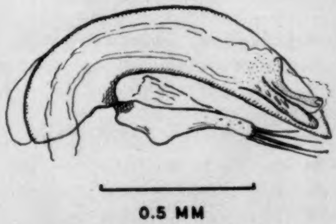


Fig. 8.—*Pseudanophthalmus tenuis blatchleyi* n. subsp. Type, Truitt's Cave, Monroe Co., Indiana; aedeagus.

the investigation of Indiana caves and their fauna and a widely known student of Indiana beetles.

YOUNGI GROUP

Pseudanophthalmus youngi youngi Krekeler

Pseudanophthalmus youngi **Krekeler 1958:175. Clifty Caves, Washington Co., Indiana (Chicago Nat. Hist. Mus.).**

Known only from the type locality, located four miles N. of Campbellsburg (C. H. Krekeler, 1950; T. C. B., 1957).

Pseudanophthalmus youngi donaldsoni Krekeler
Fig. 2

Pseudanophthalmus donaldsoni **Krekeler 1958:175. Type: Donaldson Cave complex, Lawrence Co., Indiana (Chicago Nat. Hist. Mus.).**

Known only from the type locality, Donaldson, Bronson, and Upper and Lower Twin Caves, in Spring Mill State Park (C. H. Krekeler, 1950, 1953; T. L. Poulson, 1957, 1958). The four caves have been connected by direct exploration. The Donaldson population differs in minor respects from the Clifty population, eight miles distant. The differences cited by Krekeler (1958) were found relatively consistent in the writer's samples from both caves.

The transfer apparatus of *youngi* (Fig. 2) is one of the most complex within the genus. The left dorsal copulatory piece is a somewhat flattened rod, the left edge of which is heavily sclerotized and folded. The right ventral piece forms about two-thirds of a tube beneath the left piece; the apex is shaped like the bow of a canoe, a small hamulate process extending slightly beyond the apex of the left piece.

SHILOHENSIS GROUP

Pseudanophthalmus shilohensis shilohensis Krekeler
Fig. 3

Pseudanophthalmus shilohensis **Krekeler 1958:178. Type: Shiloh Church Cave, Lawrence Co., Indiana (Chicago Nat. Hist. Mus.).**

P. s. shilohensis is known from three caves in Lawrence County: Shiloh Church Cave, near Eureka Springs (C. H. Krekeler, 1949, 1950; Catherine K. Barr and T. C. B., 1957); Donnehue's Cave, a mile S. of Bedford (T. C. B., 1957); and Hert Hollow Cave, two miles SW. of Springville (one female, T. C. B., 1957). The specimen from Hert Hollow Cave is tentatively referred to this subspecies until males can be collected.

The transfer apparatus of *shilohensis* (Fig. 3) is diagnostic, though its position within the median lobe renders it difficult, if not impossible, to interpret in whole mounts of the aedeagus. It consists of left dorsal and right ventral copulatory pieces, both spatulate and ventrally concave, the left dorsal piece smaller and nested within the right ventral piece, forming a wide spout.

Pseudanophthalmus shilohensis mayfieldensis Krekeler

Pseudanophthalmus mayfieldensis Krekeler 1958:178. Type: Mayfield's Cave, Monroe Co., Indiana (Chicago Nat. Hist. Mus.).

P. s. mayfieldensis inhabits the caves of Monroe County in the vicinity of Bloomington. The type locality, Mayfield's Cave, was studied extensively in the classic investigations of Banta (1907), who stated that this beetle (determined as "Anophthalmus tenuis") was "fairly common" but "not abundant." Ten specimens were collected crawling about among cobbles, beneath which flowed a very shallow branch of the cave stream (August, 1957, Heiner Hoffman and T. C. B.). One male was collected in May's Cave, Monroe County (August, 1957, T. C. B.). Specimens from Truitt's Cave, Monroe County, were examined in the U. S. National Museum collection, and are referred to *P. s. mayfieldensis.* This subspecies differs from *P. s. shilohensis* principally in the wider pronotum and in having usually three (four in *shilohensis*) setae on the parameres. The apical recurrent stria may be connected directly with the third longitudinal stria or flared laterally toward the fifth stria, though aedeagi of both variants are indistinguishable. Only the latter strial condition obtains in the writer's series of eighteen *P. s. shilohensis.*

Pseudanophthalmus shilohensis boonensis Krekeler

Pseudanophthalmus boonensis Krekeler 1958:180. Type: Boone's Cave, Owen Co., Indiana (Chicago Nat. Hist. Mus.).

P. s. boonensis has been collected only in Boone's Cave, a mile N. of Freeman (C. H. Krekeler, 1950; T. C. Barr, 1957, one female). The type series consists of only three specimens. The type cave is behind the terminal moraine of the Illinois glacier, indicating that this beetle colonized its present habitat no earlier than Sangamon time.

DISCUSSION

Externally, *tenuis, shilohensis,* and *youngi* share several features suggestive of close relationship: (a) elongate, rather convex body and slender appendages; (b) median lobe of labrum prominent; (c) pronotum narrowed in basal third, posterior angles acute and produced beyond the base; (d) shallow longitudinal striae on the elytra; and (e) short, usually rounded apical recurrent striae, running alternately to the third or the fifth longitudinal stria. All have a slender, strongly arcuate aedeagus, the apex of which is usually only briefly attenuate. The greatest divergence occurs in the transfer apparatus. Even here the similarities are striking — the right piece is a large, medially concave membrane, strongly sclerotized at the base, partially enveloping the smaller left piece. This relationship is rendered clear by studying the transfer apparatus apart from the median lobe, and in *youngi* and *shilohensis,* allowing for a 90° rotation from the normal position as

found in *tenuis.* A close common ancestry for all three species is indicated.

The *eremita* group seems most closely related to the *robustus* group of *Pseudanophthalmus,* species of which inhabit caves of the Eastern Highland Rim and the western margin of the Cumberland Plateau in Tennessee and southern Kentucky. It resembles *robustus* itself in the robust, depressed form; the position of the first discal seta; the large, rounded, apical stria; and especially in the shape of the aedeagus and the nature of the transfer apparatus. It differs in the virtual absence of longitudinal elytral striation; the slightly greater development of pubescence; and the close spacing of the humeral marginal setae. There are also minor but possibly significant differences in the shape of the apical stria and in the relative lengths and sizes of the copulatory pieces.

A nearer relationship geographically, if somewhat more distant morphologically, is perhaps to be sought in *Pseudanophthalmus* of the *menetriesi* group, which possess an elongate, flattened right copulatory piece with thickened edges, and a rod-like left piece the apex of which is slightly enlarged. Specimens unquestionably related to *P. menetriesi* have been collected from Hardin County, Kentucky, southward and eastward to Clay County, Tennessee.

P. leonae appears to be an intermediate form in some measure uniting the major characteristics of both the *tenuis-shilohensis-youngi* aedeagus and that of the *eremita-robustus-menetriesi* line. In the robust, depressed body form, the low median lobe of the labrum, and the shape of the pronotum, *leonae* resembles *eremita* and *emersoni,* but the lamellar (probably membranous) right copulatory piece and the small, rod-like left piece bespeak a distant tie with *tenuis.*

The great variety of genital types of *Pseudanophthalmus* within a small area is a striking characteristic of the Mitchell plain assemblage. Five species groups are compressed into a region 100 miles long by 25 miles wide. This variety attains a maximum in Lawrence County, toward the northern terminus of the region, where all five groups are present. For a possible explanation of this phenomenon one may consider the factors influencing cave colonization by trechine beetles. Jeannel (1949) suggested that the cool, moist glacial climates favored the geographic expansion of the trechines, and that environmental conditions were most favorable at the very periphery of the ice sheets. During the warmer, drier interglacials the trechines retreated to the summits of the Appalachians, to the north, or into caves. Although we could expect cave colonization by these beetles in any major limestone area climatologically affected by the ice sheets, it seems probable that the greatest diversity of surface species would occur near the edge of the ice, and that in such regions the possibility for colonization of caves by a maximum number of species would be greatest. In eastern North America the Mitchell plain — a northward extension of the great cave region of Kentucky, Tennessee, and Alabama — is the only major cave area bordering a terminal moraine of a Pleistocene ice sheet, and would have afforded numerous caves for colonization

by cryptozoic beetles. It is suggested that the Mitchell plain species of *Pseudanophthalmus* represent the remnants of a rich periglacial fauna, and that their diversity is the direct result of the optimum environmental conditions which prevailed at the margins of the Illinois and/or Wisconsin ice sheets.

If this hypothesis be correct, we may expect the discovery of additional new and unusual trechines in caves of the Mitchell plain. It would not be surprising if these forms prove to be quite rare or limited in distribution, like *eremita, emersoni,* and *leonae.* If their ecological niches do not in fact coincide with those of abundant, wide-ranging species like *P. tenuis* and *P. shilohensis,* there must at least be considerable overlap, resulting in intense competition with apparently more successful species. This interpretation suggests as its corollary that the rare, localized species (*eremita, emersoni,* and *leonae*) are moribund stocks close to extinction.

REFERENCES

BARR, THOMAS C., JR. 1959. New cave beetles (Carabidae, Trechini) from Tennessee and Kentucky. *Jour. Tenn. Acad. Sci.,* **34**:5-30.

HORN, GEORGE H. 1871. Description of new Coleoptera of the United States. *Trans. American Ent. Soc.,* **3**:325-344.

———1883. Miscellaneous notes and short studies of North American Coleoptera. *Ibid.,* **10**:269-312.

JEANNEL, R. 1923-1928. *Monographie des Trechinae.* L'Abeille 32, 33, 35.

———1931. Révision des Trechinae de l'Amérique du Nord. *Arch. zool. exp. et gén.,* **71**:403-499.

———1949. Les coléoptères cavernicoles de la région des Appalaches. Étude systématique. *Notes Biospéologiques,* fasc. 4, *Publ. Mus. Nat. Hist. Nat. Paris,* No. **12**:37-104.

KREKELER, CARL H. 1958. Speciation in cave beetles of the genus *Pseudanophthalmus* (Coleoptera, Carabidae). *Amer. Midl. Nat.,* **59**:167-189.

LENG, CHARLES W. 1920. *Catalogue of the Coleoptera of America, North of Mexico.* 470 pp. Mt. Vernon, N.Y.

PACKARD, A. S., JR. 1888. The cave fauna of North America, with remarks on the anatomy of the brain and origin of the blind species. *Mem. Nat. Acad. Sci.,* **4**(1): 156 pp.

VALENTINE, J. MANSON 1932. A classification of the genus *Pseudanophthalmus* Jeannel (fam. Carabidae) with descriptions of new species and notes on distribution. *Jour. Elisha Mitchell Sci. Soc.,* **48**:261-280.

———1945. Speciation and raciation in *Pseudanophthalmus* (cavernicolous Carabidae). *Trans. Connecticut Acad. Arts and Sci.,* **36**:631-672.

Alteration of the Composition of Rainwater by Trees

G. K. VOIGT

School of Forestry, Yale University, New Haven, Connecticut

During a study of the distribution of rainfall on the forest floor (Voigt, 1959) it was observed that tree canopies are subject to considerable leaching by rainwater. This water ultimately reaches the soil by dripping from the foliage and small branches or it is concentrated by the branches and funneled down the stem. The former component is generally termed throughfall and the latter is designated as stemflow. Although previous studies (Stenlid 1958; Tamm, 1951; 1953) have shown that salts are removed from tree canopies by rainfall, none of these authors has considered the contribution of stemflow to this segment of the nutrient cycle. Pozdnyskov (1956) determined acidity, dry matter content and ash content of stemflow water from birch, larch and pine, but no detailed chemical analyses were given. The present investigation was concerned with the nutrient content of rainwater, its modification by three forest cover types, and with the net nutrient return to forest soils resulting from the addition of rainwater.

Acknowledgments.—The author gratefully acknowledges the helpful suggestions of Professors G. M. Furnival and F. Mergen, Yale School of Forestry.

Methods and Materials

The study area was located in southern Connecticut about eight miles east of New Haven. This area receives about 45 inches of precipitation per year, mostly as rain. Water samples were collected from two storms; one in May and one in September from four cover types: red pine (*Pinus resinosa,* Ait.), hemlock (*Tsuga canadensis* [L.] Carr.), beech (*Fagus grandifolia,* Ehrh.) and an open area. The plots were arranged along a line which measured roughly a quarter of a mile from one extreme to the other. Stemflow samples were collected from seven trees in each forest cover type and throughfall samples were collected in five rain gauges scattered on each forested plot. Total rainfall for each storm was determined by five rain gauges near the center of the open area. The latter samples were also used to determine the initial composition of rainwater. The May storm totaled 0.97 inches and the September storm totaled 1.01 inches.

Total nitrogen content of the water was determined by the Kjeldahl method within a day after collection. Nitrate nitrogen was determined by the phenoldisulfonic procedure, but since the water samples showed virtually no nitrate nitrogen, the values in Table I refer to the results of determination of Kjeldahl nitrogen which includes organic and ammonium forms. Potassium and calcium were measured with a Beckman DU flame spectrophotometer. Phosphorus

was determined colorimetrically, using the ammonium molybdate-stannous chloride method. Potassium, calcium and phosphorus determinations were made on acidified samples that had been concentrated by evaporation (Wilde and Voigt, 1959).

Results and Discussion

The composition of rainwater modified by tree canopies is compared with natural rainwater in Table I. The values for natural rainfall tend to be slightly higher than those reported previously (Tamm, 1951; 1953). Both this fact and the differences in contents of K and Ca in May and September are probably related to the close proximity of the study area to the highly industrial region of the

TABLE I.—Composition of rainwater collected under different forest cover types

COVER TYPE	MAY N ppm	MAY P ppm	MAY K ppm	MAY Ca ppm	SEPTEMBER N ppm	SEPTEMBER P ppm	SEPTEMBER K ppm	SEPTEMBER Ca ppm
Open area	0.05	0.01	0.3	0.6	0.07	0.01	0.6	0.8
Red Pine								
Throughfall	0.05	0.04	0.6	1.7	0.05	0.04	1.7	1.5
Stemflow	0.12	0.07	7.2	2.2	0.18	0.08	6.5	15.3
Hemlock								
Throughfall	0.03	0.03	0.6	1.9	0.08	0.03	2.7	2.2
Stemflow	0.10	0.05	0.8	3.0	0.11	0.08	6.3	7.8
Beech								
Throughfall	0.05	0.03	0.5	1.1	0.09	0.04	1.7	1.5
Stemflow	0.04	0.04	0.6	1.1	0.16	0.06	6.1	1.5

eastern seaboard. Differences in direction of storm movement or prevailing surface winds could conceivably cause great differences in the amount of air pollution.

It is possible that industrial contamination also contributed to the values shown for water collected under forest cover. However, both collection dates were preceded by one or more days of precipitation so that most of the dust particles from the atmosphere that had settled on the leaf surfaces had been removed. Thus, it appears that the modification in rainwater composition resulted from addition or removal of ions by the trees. Since the first sampling period corresponded roughly to the initial burst of growth and the second one to the onset of dormancy, it would appear also that the observed differences were related to seasonal variations in metabolic activity and changes in the anatomical characteristics of the leaves.

Within each sampling period the composition of the water collected as stemflow showed greater species differences than the water collected beneath the tree canopies. These differences are probably related to variations in bark texture among the species observed. Red

Table II.—Movement of nutrients in rainwater under different forest cover types

COVER TYPE	MAY				SEPTEMBER			
	N mgm	P mgm	K mgm	Ca mgm	N mgm	P mgm	K mgm	Ca mgm
Open area								
Addition to soil/acre*	5	1	30	59	6	1	59	72
Red pine								
Throughfall/tree	6.0	4.8	72.2	204.6	6.1	4.8	204.6	180.6
Stemflow/tree	0.3	0.1	17.3	5.3	0.4	0.2	15.6	36.7
Return to soil/tree	6.3	4.9	89.5	209.9	6.5	5.0	220.2	217.3
Return to soil/acre*	3	3	45	105	3	3	110	109
Tree contribution/acre*	–2	+2	+15	+44	–3	+2	+51	+37
Hemlock								
Throughfall/tree	5.1	5.1	101.4	321.2	13.7	5.0	456.5	372.0
Stemflow/tree	1.3	0.6	10.7	40.2	1.5	1.1	84.4	93.6
Return to soil/tree	6.4	5.7	112.1	361.4	15.2	6.1	540.9	465.6
Return to soil/acre*	3	3	52	166	7	3	249	214
Tree contribution/acre*	–2	+2	+22	÷97	+1	+2	+190	+142
Beech								
Throughfall/tree	13.3	8.0	133.9	294.5	24.1	10.7	455.2	401.7
Stemflow/tree	1.2	1.2	18.0	33.0	4.8	1.8	183.0	45.0
Return to soil/tree	14.5	9.2	151.9	327.5	28.9	12.5	638.2	446.7
Return to soil/acre*	5	3	49	105	9	4	204	143
Tree contribution/acre*	0	+2	+19	+44	+3	+3	+145	+71

* Values are in grams

pine and hemlock have rough bark and hence more surface area than beech on which the bark is smooth. Presumably the rough bark would also be subject to more contamination from mosses, lichens and other organisms.

The study of rainfall distribution referred to earlier (Voigt, 1959) allowed calculation of the magnitude of salt movement to show the net return to the soil under the three forest cover types studied. These data which are presented in Table II were obtained by relating the composition values from Table I to the mean amounts of water added as throughfall or stemflow under a single tree of each species. These figures were converted to the acre basis by multiplying by the appropriate number of trees per acre. It is apparent that the higher nutrient concentration in stemflow shown in Table I was outweighed by the greater amount of water added as throughfall. Therefore, water dripping through the canopy constituted a substantially greater proportion of the net soil addition than did stemflow.

Comparison of the amounts of nutrients added by rainwater to soil in the open with the return under forest trees indicates that the trees made a substantial contribution to the soil in nearly all cases. The exception to this generality was nitrogen. The returns per acre in May under red pine and hemlock and the September values for red pine were lower than the addition to the soil in the open. Apparently the foliage of the trees absorbed nitrogen from the rainwater instead of releasing it. This phenomenon was also observed by Tamm (1951), but his values referred to rainwater concentrations rather than net soil returns. The only instance in which significant amounts of nitrogen were released by the trees occurred in the samples collected under beech in September.

The values for potassium and calcium were generally higher in September than in May. The increased amounts of salts added to the soil in the open offer a partial explanation. It seems reasonable, however, that changes in the nutrient requirements accompanying the approach of dormancy are also involved. Potassium in these trees was more vulnerable to extraction by rainwater in September than in May. It is also apparent that potassium was more easily extracted than calcium in September whereas the reverse was true in May. Leaching of calcium from red pine showed a relative decrease in September, but in hemlock and beech more calcium was extracted at the end of the growing season. Although the September samples were collected well in advance of autumnal color changes, it is likely that the abscission layer had already begun to form in the beech leaves. Thus, the leaf would be essentially isolated from the tree and any nutrient transfer from leaf to tree would be reduced to a minimum. Red pine and hemlock retain their needles for three or more years so that ample opportunity would exist for nutrient transfer associated with dormancy. The observed variations in these three species undoubtedly reflect fundamental differences in their physiological processes. Superimposed on these differences was the vari-

ability which may have existed in the chemical composition of the soil.

The values in Table II are based on two storms and hence do not allow a precise estimate of total nutrient movement. It is reasonable to expect, however, that a mean value for each cover type would fall within the range indicated by the two extremes of the growing season. If one uses this assumption and an average rainfall figure of 19 inches for the growing season in Connecticut (U.S.D.A., 1941, Climate for Connecticut), approximations are obtained which indicate that the return of nitrogen and phosphorus in rainwater is of little importance. The return of potassium ranges from about two to ten pounds per acre and calcium ranges from six to nine pounds per acre during the growing season. It is likely that under species with foliage high in mineral nutrients, such as tulip poplar (*Liriodendron tulipifera,* L.), basswood (*Tilia americana,* L.), hackberry (*Celtis occidentalis,* L.) and flowering dogwood (*Cornus florida,* L.) considerably more potassium and calcium is returned to the soil (Lutz and Chandler, 1946).

It should be emphasized that these nutrient movements from the tree to the soil do not constitute independent additions to the nutrient capital. They are merely segments of the nutrient cycle which may be recirculated from the soil to the tree and back to the soil several times during the growing season. Thus, it would be misleading to conclude that from two to ten pounds of potassium and from six to nine pounds of calcium per acre are added to the soils each growing season under red pine, hemlock, or beech. Instead these figures give an indication of the extent of nutrient circulation within the soil-tree system.

SUMMARY

The contents of nitrogen, phosphorus, potassium, and calcium were determined in rainwater collected under red pine, hemlock, and beech stands, and in an open area. Throughfall and stemflow samples were taken at the beginning and end of the growing season. The results showed that the composition of the water was altered by the trees and that the degree of alteration was affected by season, species, and location of collection with respect to the tree. The nutrient contents of water collected in September were higher than in samples collected in May. Stemflow from red pine and hemlock contained more nutrient elements than did stemflow from beech. Values for nutrient content of throughfall showed practically no correlation with species and were generally lower than values for stemflow. Calculation of nutrient movement indicated that considerable amounts of potassium and calcium were extracted from the foliage and branches and returned to the forest soils. Nitrogen and phosphorus returns were about the same as those received by the soil in the open area. It is felt that an approximation of the magnitude of the annual nutrient

circulation may be obtained by extending the data from the two storms observed.

REFERENCES

LUTZ, H. J. AND R. F. CHANDLER, JR. 1946. *Forest Soils*. New York: John Wiley and Sons, Inc., pp. 146; 157.

POZDNYAKOV, L. K. 1956. [The role of rain penetrating beneath the forest canopy in the process of the exchange of material between forest and soil.] *Dokl. Akad. Nauk.*, **107**:753-756. Original not seen. Abstr. in: *Soils and Fertilizers*, **19**:379. (Abs. no. 1820).

STENLID, GÖRAN. 1958. Salt losses and redistribution of salts in higher plants. In: *Encyclopedia of Plant Physiology IV:* 615-637. Springer-Verlag. Berlin.

TAMM, C. O. 1951. Removal of plant nutrients from tree crowns by rain. *Physiol. Plant.*, **4**:184-188.

———1953. Growth yield and nutrition in carpets of a forest moss (*Hylo-conium splendens*). *Medd. Stat. Skögsforskn. Inst.* **43**:1-140.

U.S.D.A. 1941. *Yearbook of Agriculture. Climate and Man.* Washington: U. S. Govt. Print. Off., p. 993.

VOIGT, G. K. 1959. Distribution of rainfall under forest stands. *Forest Science,:* In press.

WILDE, S. A. AND G. K. VOIGT 1959. *Analysis of Soils and Plants for Foresters and Horticulturists.* Second Revised Edition. Ann Arbor: J. W. Edwards, Publisher, Inc.

Sex Ratios and Population Density in Hibernating Myotis

DONALD W. TINKLE AND WILLIAM W. MILSTEAD
Texas Technological College, Lubbock, and the University of Kansas City

This study was undertaken as a part of an investigation of the biology, parasites and migration of bats of northwestern Texas supported by the National Institute of Health through a grant to Dr. Russell W. Strandtmann of Texas Technological College. We wish to acknowledge the help of many Texas Technological College faculty and students, but we are particularly indebted to Russell Strandtmann, Jessie Hillman, Colene Amondson, Chester Rowell and John E. George. We wish to thank Messrs. J. A. Hedgecoke of Amarillo, R. W. Walkup of Lazare and F. L. Richardson of Quanah for permission to study caves located on their ranches.

The data reported here were obtained in 1958 and 1959 in three gypsum caverns located in Armstrong, Cottle and Hardeman Counties in the Texas Panhandle. These caves lie within the mesquite plains and short grass plains of the Kansas biotic province (Blair, 1954). The major objectives of the investigation were to estimate population density in bats by mark and recapture techniques and to study sex ratios to determine if they fitted the general pattern suggested by previous authors. A total of 3288 *Myotis velifer incautus* were banded during the course of this study, most of them at three caves. Exact locality data on these and other distributional records have been reported (Milstead and Tinkle, 1959).

Sex Ratio

PANTHER CAVE

This cave is located on the Floyd Richardson ranch, 22 miles southeast of Childress, Cottle County, Texas. The cave was visited on six occasions between February 15, 1958, and March 6, 1959, when large numbers of bats were present (Table I). The figures in-

TABLE I.—Variation in the sex ratio of *Myotis* at Panther Cave

Date	Total bats	% ♂♂	% ♀♀
15 Feb. 1958	143	31	69
29 March 1958	208	38	62
26 April 1958	16	63	37
14 Nov. 1958	264	55	45
8 Feb. 1959	346	32	68
6 March 1959	30	30	70

cluded both banded and unbanded bats. On one occasion when a large number (123) banded bats were recovered, the sex ratio in the banded bats was about the same as that in the unbanded ones.

There is a clear-cut decrease in the percentage of males and increase in percentage of females during the winter. The figures for the same months in two different years are nearly the same.

WALKUP CAVE

This cave, located in the R. W. Walkup ranch, 3 miles southeast of Lazare in Hardeman County, Texas, is about two miles east of Panther Cave. Considerable exchange of bats occurs between the two caves. On five visits to this cave, large numbers of bats were encountered and the sex ratio of these samples shows a clear increase in the percentage of females and a decrease in that of males (Table II).

The sex ratio of banded bats was about the same as that of the unbanded ones when sufficiently large numbers of banded bats were recovered.

SINKHOLE CAVE

This cave, located on the Hedgecoks ranch, 29 miles southwest of Claude, Armstrong County, Texas, is 100 miles northeast of the other caves and no interchange between this and the other two caves has been noted.

Large numbers of bats have been found in this cave on seven occasions and the sex ratio of these shows a decrease in males and an increase in females although not as sharply as in the other two caves (Table III).

The sex ratio of banded bats which were frequently obtained in large numbers at this cave show the same general seasonal increase in females and decrease in males.

DISCUSSION

The disparity in sex ratio in bats at various seasons is known to be extreme. Hitchcock (1950) noted an apparent decrease in the percentages of males of several species the farther south one goes, although he did find a high percentage of male *Myotis lucifugus* (65.5%) in a cave in Kentucky. Since the sex ratio is known to be

TABLE II.—Variation in the sex ratio of *Myotis* at Walkup Cave

Date	Total bats	% ♂♂	% ♀♀
18 Oct. 1958	92	61	39
8 Nov. 1958	697	42	58
5 Dec. 1958	321	43	57
7 Feb. 1959	246	37	63
6 March 1959	209	31	69

TABLE III.—Variation in the sex ratio of *Myotis* from Sinkhole Cave

Date	Total bats	% ♂♂	% ♀♀
16 Feb. 1958	129	35	65
15 Nov. 1958	117	56	44
21 Nov. 1958	375	49	51
13 Dec. 1958	319	48	52
21 Feb. 1959	813	38	62
1 March 1959	118	40	60
21 March 1959	336	38	62

equal at birth, some other explanation of the disparity is necessitated. Rice (1957) in a study of *Myotis austroriparius* in Florida found that these bats show an increase in males in the spring and early summer and a decrease in the fall. Females always outnumbered males, however, by more than two to one. He examined data of this species presented by other authors and concluded, like Hitchcock, that the proportion of males was less in the south. Most authors (Hitchcock, *op. cit.;* Griffin, 1940; Mohr, 1945; Eisenstraut, 1947) report that populations of bats hibernating in caves contain a preponderance of males.

Davis (1959) studied disproportionate sex ratios in 4,000 hibernating *Pipistrellus subflavus* in 48 West Virginia caves and concluded that the percentage of females in the population increased as one went south. He suggested that the sex ratio may reflect the severity of the winter — the harsher the winter, the more males that overwinter in the cave. This accentuates the slightly greater female mortality and the tendency of females to winter outside the caves. His hypothesis would explain the extremely high percentage (over 90) of males reported in the far northern populations by Hitchcock (1950) and others where climatic conditions are more severe than in the south.

Rice (1957) in a study of *Myotis austroriparius* in Florida found that females always greatly outnumber males. His figures on sex ratio when compared with those on this same species from other areas show a decrease in the percentage of males from 71 percent in Indiana to 25 percent in Louisiana.

Eisenstraut (1947) banded 4890 *Myotis myotis* in Germany without noting the sex ratio and followed these bats as they returned to the cave in which they were banded for 11 years. His data on these banded bats show a preponderance of males for the first seven years, after which the sex ratios became equalized by the tenth year. He also found that the mortality rate of the females was higher than that of males.

Pearson, *et al.* (1952) found that the percentage of male *Corynorhinus rafinesquei* in California was higher in the sections of the state having a harsher winter. These data again suggest that climatic conditions may play an important role in regulating the sex ratio of cavern-dwelling bats.

Our data for three caves show clearly that the sex ratios are most nearly equal in the late fall, presumably when the bats are mating; after this period there is a steady decline in the percentage of males and an increase in females throughout the winter until the bats leave the caves in late winter and early spring. These data support the views of other authors in that the caves studied by us are in the southern United States in an area of moderate climatic conditions and contain a low percentage of males in the winter.

Several explanations for the change in sex ratio through the winter are possible:

1. Bats apparently arrive in the colony during the winter and are predominantly females. Griffin (1945) found that *Myotis* in New England moved about extensively from one cave to another during the winter months.

2. There is greater mortality among males than among females. We have no data as yet on mortality. Some studies of other bats have suggested slightly greater female mortality, others greater male mortality, with no very significant differences in any case, except possibly in *Myotis myotis* in Europe (Eisenstraut, 1947) in which female mortality was significantly greater than male.

3. A greater proportion of males than females emigrate during the winter for reasons of conditions within the caves or because of disturbance due to banding. How much this influences sex ratios can be determined by studying the sex ratio of bats that were banded at each cave, but never recovered, assuming that these bats left soon after their initial capture.

   These data show that of 302 bats banded at Sinkhole cave and never recovered, 137 (45%) were males. Of 211 not recovered at Panther Cave, 69 (33%) were males and of 616 not recovered at Walkup Cave, 293 (48%) were males. Clearly, there is not a greater number of male than female bats leaving the caves, so the disproportionment of sex ratios must be due to differential emigration or mortality within the cave.

It is of interest that Twente (1955a) showed that males of *Myotis velifer* were generally more abundant than females in the gypsum caverns he studied in south central Kansas and northwestern Oklahoma. The winters in that area are more severe and a greater percentage of males would be expected following the hypothesis of Davis (1959). Twente (*op. cit.*) also found, as we did, that sex ratios were more nearly equal in late October and November.

POPULATION DENSITY

Almost no published data on population density in bats are available. Those figures that have been published (Twente, 1955; Rice, 1957; Pearson, Koford and Pearson, 1952) are based on measurements of clusters and calculations of the number of bats per some unit of area.

Because it was felt that we were working with bat populations of a relatively small size, we were confident that mark and recapture data would give some idea of seasonal changes in population density. Two methods of density determinations were used. One of these was a Lincoln Index constructed as follows:

$$\frac{\text{No. of bats banded in precensus}}{\text{X (other bats present)}} = \frac{\text{No. of banded bats found in census}}{\text{No. of unbanded bats in census}}$$

$$\text{Population size} = \text{X} + \text{number banded in precensus}$$

The second method used was that of Hayne (1949) in which the population of any given time is based on the equation $P = \frac{\Sigma WX^2}{\Sigma WXY}$ in which W is the total number of marked and unmarked bats caught on each trip, X is the number previously marked and released and Y is the proportion of marked animals on each trip.

PANTHER CAVE

The mark and recapture data at Panther Cave are fewer than for the others. Only a few estimates can be made (Table IV).

Because Lincoln indices are based partly on succeeding figures while Hayne indices are based on preceding ones, one would expect the Lincoln Index of one trip to most closely match the Hayne Index for the next succeeding trip. The table shows a close approximation in the figures considering the above statement. There are too many gaps between trips for the data to be accurate unless little or no immigration or emigration occurred, but it is likely that considerable of both takes place.

TABLE IV.—Population estimation of *Myotis* in Panther Cave

Date	Lincoln	Hayne	Number seen	% of sample that was banded
15 Feb. 1958	1190	......	143	0
29 March 1958	......	1192	208	12
14 Nov. 1958	708	......	264	0
8 Feb. 1959	588	713	346	37
6 March 1959	......	736	34	59

TABLE V.—Population estimation of *Myotis* in Walkup Cave

Date	Lincoln	Hayne	No. of bats seen	% of sample that was banded
18 Oct. 1958	1173	......	92	0
8 Nov. 1958	1257	1137	697	8
5 Dec.. 1958	1350	1646	325	18
7 Feb. 1959	306	2107	245	24
6 March 1959	......	1886	209	44

WALKUP CAVE

The data on population density of *Myotis* in Walkup Cave are more extensive (Table V).

The actual numbers of bats seen indicated a buildup in population in the early winter and a steady decline thenceforth, but the indices do not indicate a decline in numbers until much later. The indices generally indicate bat numbers in the cave far exceeding what we have ever actually encountered. Since both of these indices will give high figures if there is a great deal of population turnover, this is taken as additional evidence that immigration and emigration of bats takes place throughout the winter.

SINKHOLE CAVE

All of the data on population densities of *Myotis* at this cave are from one winter, 1958-1959 (Table VI).

In this cave the figures based on Lincoln Index show a steady decline in numbers from late November while the Hayne Index shows a relatively steady increase. The actual number of bats found indicates a build-up in population until December and a decline thereafter. We were not always confident that every bat had been removed from the cave, but an intensive effort was made to do this on the last three trips and a fair degree of success is indicated by

TABLE VI.—Population estimation of *Myotis* in Sinkhole Cave

Date	Lincoln	Hayne	No. of bats seen	% of bats that had been banded
15 Nov. 1958	476	......	121	28
21 Nov. 1958	1654	483	399	18
13 Dec. 1958	1288	1639	891	24
21 Feb. 1959	1161	1797	825	27
1 March 1959	318	1707	197	71
21 March 1959	......	1839	338	62

the rapid increase of the percentage of banded from 27 percent on Feb. 21 to 71 percent on Mar. 1.

The fact that more bats and a smaller percentage of banded were found on March 21 than on March 1 is explained by assuming that bats are in the process of leaving the caves in the area and that a number of migratory transients stopped briefly at this cave en route to summer quarters which are as yet undiscovered.

For the first two estimates the figures for the two indices are very nearly the same, but after this there is an increasing disparity in the figures. In general the Lincoln Index figures are closer to the actual number of bats seen and since it is not based on cumulative figures it is probably more reliable than the Hayne Index which will be more greatly affected by emigration and immigration because it is based on cumulative figures.

If a cave were visited three days during one week and then left for several weeks and then again sampled for three days, the discrepancies in the figures that are due to emigration and immigration would be minimized and it is felt that reliable figures on seasonal variation in density could be obtained in this way. For this purpose the Lincoln Index may yield more reliable results.

SUMMARY

Sex ratios and population densities of *Myotis velifer incautus* in three hibernating cave colonies in northwest Texas were studied.

There is a near equal sex ratio only in the late fall or early winter presumably following mating. After this there is a steady decrease in the percentage of males and an increase in females. This is interpreted to mean there is a greater immigration of females than males into the colony throughout the winter. The percentage of males falls to about 30 percent in all three caves by the late winter and early spring when the bats leave all three caves.

Population densities were estimated by Lincoln and Hayne indices. The figures by the two methods were sometimes in close agreement, but were often widely disparate. Generally, the Hayne Index figures indicate population numbers which are felt to be too high on the basis of the actual number of bats encountered on each trip.

The Lincoln Index seems to yield more reasonable estimates, compared with the total number of banded and unbanded bats actually caught, and it is suggested that both estimates would be more accurate if the data were obtained on several successive days at a few periods of the year so that gaps between the precensus and census periods are greatly reduced.

REFERENCES

BLAIR, W. FRANK 1954. Mammals of the Mesquite Plains Biotic District in Texas and Oklahoma and speciation in the central grasslands. *Tex. Jour. Sci.*, **1954**(3):235-264.

DAVIS, WAYNE H. 1959. Disproportionate sex ratios in hibernating bats. *J. Mamm.*, **40**(1):16-19.

EISENSTRAUT, M. 1947. Die mit Hilfe der Beringungsmethode erzielten Ergebnisse über Lebensdauer und jahrliche Verlustziffern bei *Myotis myotis* Borkh. *Experimentia*, **3**:157-158.

GRIFFIN, DONALD R. 1940. Notes on the life histories of New England cave Bats. *J. Mamm.*, **21**(2):181-187.

———1945. Travels of banded cave bats. *Ibid.*, **26**(1):15-23.

HAYNE, DON W. 1949. Two methods for estimating population from trapping records. *Ibid.*, **30**(4):399-411.

HITCHCOCK, HAROLD B. 1950. Sex ratio in hibernating rats. *Bull. Nat. Speleol. Soc.*, **10**:26-28.

MILSTEAD, WILLIAM W. AND DONALD W. TINKLE 1959. Seasonal occurrence and abundance of bats (Chiroptera) in northwestern Texas. *The Southwestern Naturalist*, **4**(3):134-142.

MOHR, CHARLES E. 1945. Sex ratios of bats in Pennsylvania. *Proc. Penna. Acad. Sci.*, **19**:65.

PEARSON, OLIVER P., MARY R. KOFORD, AND ANITA K. PEARSON 1952. Reproduction of the lump-nosed bat (*Corynorhinus rafinesquei*) in California. *J. Mamm.*, **33**(3):273-320.

RICE, DALE W. 1957. Life history and ecology of *Myotis austroriparius* in Florida. *Ibid.*, **38**(1):15-32

TWENTE, JOHN W. 1955a. Aspects of a population study of cavern-dwelling bats. *Ibid.*, **36**(3):379-390.

———.1955b. Some aspects of habitat selection and other behavior of cavern-dwelling bats. *Ecology*, **36**(4):706-732.

Seventeen New Species in the Genus Priocnessus (Hymenoptera: Psammocharidae) with Keys to Males and Females of All Known Neotropical Species

R. R. DREISBACH
Midland, Michigan

There are at present only 6 known Nearctic species in *Priocnessus*. The genus has many more species in the Neotropics. Of the 17 new species described in this paper, 12 are based on females, 3 on males, and 2 on specimens of both sexes.[1] Twenty-seven species are represented in the keys given here for the Neotropical region.

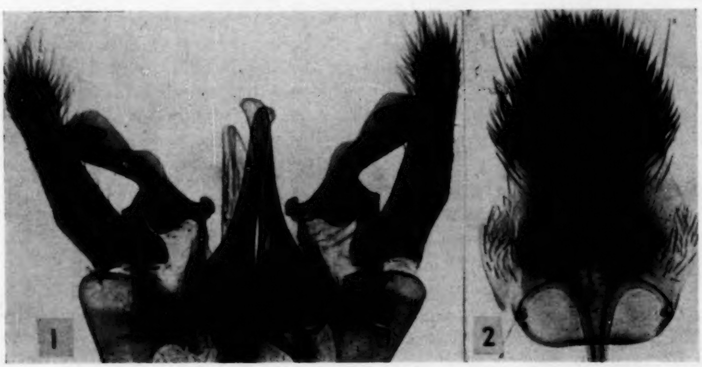
The Genus Priocnessus Banks

Wings with long narrow marginal cell, with apex acute, about 0.5 its length from wing tips; 3rd cubital 1.3 to 1.5 longer than 2nd and wider, both much longer on cubitus than on marginal vein; basal vein basad of transverse by equal to or more than length of transverse; subdiscoidal in rear wings, barely interstitial to 4 or 5 times thickness of vein apicad of cubitus; clypeus raised above mouth parts, truncate or concave with a tooth in middle of front, about 2.0 as broad as long; interior orbits parallel or slightly converging at vertex; head slightly broader than long; pronotum very short on dorsal surface; metapostnotum almost always well evident, 0.3 to 0.5 as long as postscutellum; propodum not long, in a low curve, hardly any declivity; posterior tibiae of female with 2 rows of teeth on dorsal surface, broad, flat, thin, teeth (really rectangular plates) set crosswise of length, the ones on inner edge the larger; a spine about twice their length set just behind them and touching; the teeth in outer row smaller but often the spines almost as long; the teeth sloping backward and giving a concave appearance; the space between teeth covered with fairly long not dense hair; claws in female with a small sharp tooth about center of claw and a long sharp ray, last joint of posterior tarsi generally with a few spines on ventral surface, sometimes hardly evident; males with split teeth on claws, the inner generally short, and blunt, the outer ray sharp; some species have the posterior tibiae of the males with good spines and sometimes even small teeth.

[1] The designations for places of deposit of the type specimens in this paper are as follows: *MCZ* = Museum of Comparative Zoology, Harvard University; USNM = U.S. National Museum, Washington, D. C.; *RRD* = R. R. Dreisbach, Midland, Michigan; *Howden* = Dr. Henry F. Howden, Division of Entomology, Science Service, Ottawa, Canada; *Hurd* = Dr. Paul D. Hurd, Jr., Dept. of Entomology, University of California, Berkeley 4, California.

Priocnessus hondurensis n. sp.
Figs. 1, 2.

Holotype male.—Completely black over whole body, except apex of mandibles are reddish; head and thorax very hairy, hair very long from one-half to as long as the length of first two antennal joints; the abdomen with long hair on first tergite and at apex of last three, the ventral surface with a few long hairs on all sternites; head and thorax opaque, abdomen shining; from in front vertex even with top of eyes; head slightly longer than broad; interocular distance 0.6 the transfacial; width of vertex barely slightly longer than distance between eyes at clypeus; clypeus seven-twelfths as long as width; ocelli small in a small triangle, the lateral ones about three diameters from each other, and 3.5 as far from eyes as each other; antennae black, slender, and ratio of first four joints are as 15:8:28:28; clypeus almost truncate at apex and convex on sides, a shining rim on front extending around sides; the eyes reach the vertex; pronotum very short hardly any dorsal part, posterior edge arcuate; postnotum as long as postscutellum and transversly ridged; propodeum short and in a very low curve to apex; wings reddish, apex beyond cells blackish, and the rear edge blackish to base of third discoidal cell; marginal cell very long, its distance to wing tip one-fourth its length; about as wide as second cubital cell; second cubital cell longer than wide, as long on marginal vein as on base, receiving first recurrent vein at middle; third, cubital cell longer than the second, about two-thirds as long on marginal vein as on its base and receiving second recurrent vein before middle; basal vein basad of transverse vein by about the length of the latter; in the rear wings subdiscoidal vein is interstitial with the cubitus; claws split and the inner ray blunt, heavy, less than one-half length of the slender long sharp outer ray; longer spur of posterior tibiae more than one-half



Figs. 1 and 2.—*Priocnessus hondurensis* n. sp. 1.—Genitalia (x 15). 2.—Subgenital plate (x 30).

Figs. 3 and 4.—*Priocnessus octomaculatus* n. sp. 3.—Genitalia (x 30). 4.—Subgenital plate (x 30).

length of its metatarsal joint; genitalia with parameres well and long haired on the concave inside, longer than the other parts; volsellae with a large blunt hook or flange at apex on inside; parapenial lobes slightly longer than aedeagus; subgenital plate notched near middle on sides with a slightly elevated basal triangular flat surface.

Length head and thorax 6.6 mm, abdomen approximately same length, fore wing 13.3 mm, rear wing 9.9 mm, genitalia length 1.25 mm, width 1.3 mm, subgenital plate length 1.8 mm, width 0.86 mm.

Type Locality.—Tela, Honduras. April. Bates (*MCZ*).

Priocnessus octomaculatus n. sp.
Figs. 3, 4.

Holotype male.—Body black, one-third of sides of clypeus, the anterior orbits broadly (from base of clypeus up to antennae) extending almost to top of eyes, each side of pronotum just before posterior border, a spot on middle of scutellum, posterior tip of propodeal side pieces (just above posterior coxae), a spot just in front of middle coxae, a spot each side on first tergite just before posterior edge, a spot in middle of first tergite, a very large spot on sides of second tergite, a large spot on sides of third tergite (almost touching in center), a large spot on sides of fourth tergite (almost hidden under telescoped tergite), the apex of all the femora, a narrow stripe on outside of fore tibiae, a broader stripe on outside edge of middle tibiae and the whole outside edge of posterior tibiae, whitish yellow. Mandibles whitish about center on inside edge; eyes reach vertex, the latter almost straight across but ocelli a little higher; temples very narrow, a small whitish spot just below vertex; clypeus very much raised, concave on front with a small tooth in center; numerous upright colored hairs on head, thorax, and propodeum; clypeus, thorax, coxae and legs with prostrate silvery pubescence; middle interocular 0.55 the transfacial distance; head as broad as long; lower and upper interocular distance equal; lateral ocelli two and one-half times as far from eyes as each other; antennae black, ratio of length of first four joints are as 15:6:17:20, very

slender; under side of antennae brown; top of head finely punctured; pronotum exceptionally short, hardly any dorsal surface, angulate on posterior edge; dorsal surface of thorex finely punctured, mesonotum more coarsely than the rest; postnotum about one-half as long as post-scutellum, cross ridged; propodeum short and whole length only slightly sloping; abdomen widest at apex of second tergite, there three times as wide as base of first tergite; upright hair on first tergite and a good deal on apex of last three tergites; wings almost hyaline but with a yellowish tinge in reflection; marginal cell long, one-half its length from wing tip, slightly wider than second cubital cell; third cell longer and broader than second cubital; second cubital cell about two-thirds as long on marginal vein as on cubitus, third about one-half as long; basal vein basad of transverse by the length of latter; in rear wings the subdiscoidal and cubital veins are interstitial; all spurs white, the longest spur of posterior legs about three-forths as long as basi-tarsus; very large arolia between claws.

Length head and thorax 5.3 mm, abdomen 5.3 mm, fore wings 9.9 mm, rear wings 7.0 mm, length genitalia 1.2 mm, width 1.0 mm, length subgenital plate 0.6 mm, width 0.46 mm.

Parts of genitalia all very short, aedeagus hardly 0.75 as long as volsellae, and the basal half hardly narrower than the apical half; parameres with a broad shallow concavity on inside basal half, rather sharp pointed; subgenital plate roof shaped, very broadly at base and tapering out at apex; widest above middle.

Type Locality.—Tepoztlan, Morelos, Mexico, August 20, 1956. R. R. and K. Dreisbach. (*USNM*).

Allotype female.—Markings as in the male; clypeus high, concave on apical edge with tooth in middle; interocular distance is 0.54 trans-facial, upper and lower interocular distances equal; head about 1.2 as wide as long; clypeus about 0.7 as long as wide; ratio first four antennal joints is as 12:4:18:14; third antennal joint about 0.9 the interocular distance at vertex; lateral ocelli about 1.75 as far from eyes as from each other; antennae long and slender; posterior orbits very narrow; about seven large teeth on posterior edge of hind tibiae; middle tibial joint with golden spines on posterior surface one-third to one-half width of joint; the teeth on posterior tibiae set near inner edge and a row of smaller teeth on outer edge, the space between bare and some-what concave; the large teeth set at an angle to the longitudinal length; the posterior edge of hind tibiae and the hair brush on inside yellow; the spurs white; spur of posterior tibiae one-half length of its metatarsal joint.

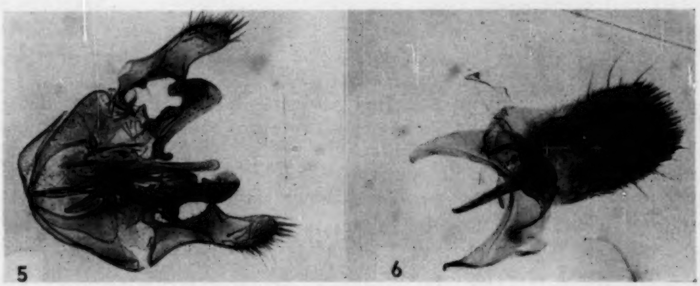
Length head and thorax 7.0 mm, abdomen 5.5 mm, fore wing 10.6 mm, rear wing 8.0 mm.

Other Localities.—Allotype female: Tepoztlan, Morelos, Mexico, August 20, 1956, R. R. and K. N. Dreisbach (*USNM*). Paratype females: two, Tepoztlan, Morelos, Mexico, September 26, 1957, R. R. and K. N. Dreisbach (*RRD*); two, Cuernavaca, Morelos, Mexico, September 29, 1957, R. R. and K. N. Dreisbach (*RRD, MCZ*); one, Carapu, Michoan, Mexico, September 2,

1938, L. J. Lipovsky (*USNM*); one, 8 miles NE. Taxco, Guerrero, Mexico, August 8, 1954, 5450 ft., Univ. Kansas, Mex. Exp. (*Univ. Kansas*).

Priocnessus orbiculatus (Smith)
Figs. 5, 6.

Body color black (particularly the thorax which is wholly black) with the thorax covered with a very beautiful fine silvery pubescence which in reflected light has a golden tinge; clypeus (except a linear black mark in middle, which extends to base of antennae), broad inner orbits which extends beyond fore ocellus, posterior orbits (broader in upper part), two preapical spots on sides of first tergite, posterior edge of first tergite, two broad spots on middle of sides of second tergite, same on third tergite and in addition a narrow band across posterior edge, a spot on middle of posterior edge of fourth tergite, apical bands across posterior edge of tergites five and six, and all of tergite seven, yellowish red; ventral surface of all coxae whitish; apex of trochanters, and all legs reddish yellow except last one or two tarsal joints of middle tarsi and all tarsal joints of posterior tarsi are blackish; antennae more or less blackish on dorsal surface and all of joint two black, underside reddish yellow except some black on last three or four joints; the first seven joints of antennae almost cylindrical, the eighth through tenth joints slightly hollowed out on under side, while the last three joints are increasingly flattened (hence the name) until the last joint is twice as wide as joints preceding the eleventh joint; clypeus strongly concave with a blunt tooth in the middle, strongly arched longitudinally, twice as broad as long; when seen from in front vertex straight across, the ocellar triangle slightly higher; the upper interocular distance 0.9 the lower interocular distance; the middle interocular distance 0.52 the transfacial distance; head approximately 1.2 as broad as long; lateral ocelli 1.5 as far from eyes as each other; ratio length first four antennal joints 12:3:18:16; very narrow posterior orbits; hardly any dorsal part to pronotum, transverse on posterior border; propodeum in sloping line



Figs. 5 and 6.—*Priocnessus orbiculatus* (Smith). 5.—Genitalia (x 30). 6.—Subgenital plate (x 30).

to apex, apex hardly lower than base, very heavily haired; whole thorax with numerous long upright hairs, fewer on abdomen; marginal long, one-half its length from apex of wing; basal vein in fore wing basad of the transverse by just about the length of the latter; in rear wing the subdiscoidal vein is just barely apicad of origin of cubitus; third cubital cell longer and broader than the second, extends nearer tip of wing than the marginal cell; inner claw of fore tarsi modified; the inner cleft part of the outer claw with broad base and the apical ray very close to it, the apical ray hardly curved on inside; the inner claw not so broad and considerable distance between the rays, the inner apical ray with deep curvature at base.

Length head and thorax 6.0 mm, length abdomen 6.0 mm, length fore wings 10.0 mm, length rear wings 7.2 mm, length genitalia 1.52 mm, width 1.06 mm, length subgenital 1.32 mm, width 0.53 mm.

The subgenital plate almost parallel-sided; the whole ventral surface of plate slightly raised above the sides; long haired around apex; the apical part of parameres apicad of the concavity on the inside longer than in other species (one-half the length of part).

Range.—El Salvador, Mexico.

Priocnessus flavidus n. sp.

Holotype female.—Black, whitish and yellowish; clypeus, face and front yellowish white, a black line from base of antennae to fore ocellus, the whole ocellar triangle and a line across vertex black; posterior orbits yellow with the back of head black; pronotum yellow except a black streak across the rise, posterior edge transverse; a large yellowish spot in middle of mesonotum over whole of scutellum except sides, a large yellowish spot under posterior wing and one each above middle and rear coxae, rest of thorax black; first tergite yellow with some black at base, second tergite with two large spots on side and posterior edge yellowish red; apical halves at least of tergites 3-6 reddish; first ventrite reddish, and posterior edge of rest of ventrite slightly reddish; coxae and trochanters whitish with some black; legs all reddish except tarsal joints are blackish; first two antennal joints and basal three-fourths of third joint yellowish, from there to apex black on dorsal surface brownish on ventral surface; clypeus with a blunt tooth in center of apex with sides concave each side of it; clypeus 2.25 times as wide as long, not very much arched on dorsal surface; lower interocular distance 1.2 times the upper interocular distance; interocular distance at middle 0.5 the transfacial distance; ratio lengths first four joints antennae are 14:5:24:20; the third antennal joint is almost 1.1 as long as width of vertex; head only very slightly broader than long; posterior orbits very narrow; lateral ocelli slightly more than 2.5 as far from eyes as each other; very short dorsal surface to the pronotum and not raised very high above neck; scutellum almost one third as long as mesonotum, raised, roof-shaped; propodeum in a very low slope; abdomen almost flat on dorsal surface and sides parallel from

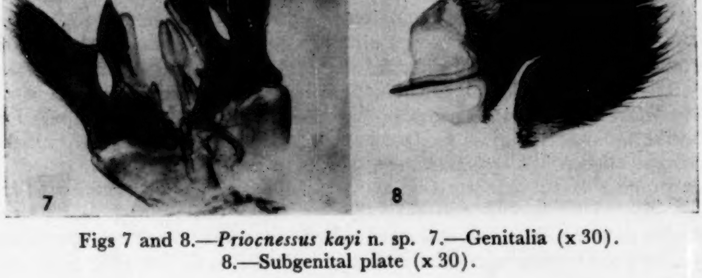
middle of second tergites to almost tip of third; head and thorax, especially the propodeum with long abundant light hair; the light spots rendered silvery by reflection by the prostrate pubescence; posterior tibiae with a row of about 10 flat, rounded, thin, teeth, set crosswise of tibiae near inner edge, with a sharp longer tooth or spine set just behind them, the outer edge with a row of similar smaller teeth; claws with a sharp tooth near the middle; the space between the two rows of teeth and around them covered with long golden hairs; marginal cell 0.6 of its length from wing tip, the cell about same width as second cubital cell, rather narrow; third cubital cell very long almost twice as long as second and extends beyond marginal cell; first recurrent vein meets second cubital cell at apical third and second recurrent meets third cubital cell at basal third, both veins almost straight; the basal vein in fore wings apicad of transverse vein by 1.5 the length of latter (which is very short); in rear wings subdiscoidal vein is barely apicad (almost interstitial) of origin of cubitus.

Length head and thorax 8.6 mm, length abdomen 6.7 mm, length fore wing 13.3 mm, length rear wing 9.3 mm.

Type Locality.—Rosario, Acatlan, El Salvador, July 22, 1955, 631 - 305 M.S.V. (*USNM*).

Priocnessus kayi n. sp.
Figs. 7, 8.

Holotype male.—Body black, head and thorax somewhat opaque, abdomen slightly shining; inner orbits to just above antennae, under side of third and fourth antennal joints, all of joints five through eight, under side of joints nine through twelve, tip of fore and middle femora inside of fore tibiae and posterior tarsal joints, light yellow; outside of fore tibiae, fore and middle tarsal joints, more or less blackish mixed with light reddish; face ventral parts of coxae and parts of thorax covered with brownish pubescence; head and thorax covered with fairly long dark hair; propodeum, first tergite, last two or three tergites



Figs 7 and 8.—*Priocnessus kayi* n. sp. 7.—Genitalia (x 30).
8.—Subgenital plate (x 30).

and ventral part of abdomen with upright hair; clypeus with a large blunt tooth in middle of apex each side of which is deeply concave with two broad teeth each side; the sides of clypeus oblique, converging toward the front so that apical edge from the outside of the lateral teeth is only one-half width of basal edge, clypeus somewhat shining; the greatest width of clypeus is twice the length; the upper and lower interocular distance just about equal; middle interocular distance is equal to 0.51 transfacial distance; width of head equal to 1.1 the length; the lateral ocelli about twice as far from eyes as from each other; ocelli of equal size; ratio of first four joints of antennae are as 10:2:12:11; antennal joints 6 -8 have a lengthwise groove on inside and joints 9 -10 have a ridge on side; pronotum short, slightly angulate on posterior border; scutellum prominent, about twice as long as postscutellum which again is almost twice as long as metapostnotum, the latter slightly, transversely ridged; propodeum sloping from base to apex; wings rather reddish yellow with mottling or a slight dark band from marginal cell backward into the third discoidal; the apex of wings from tip of marginal cell to base of subdiscoidal vein blackish, the two dark areas giving a very prominent banded effect; tip of rear wing blackish, but not the rear edge; veins yellow but are darker in blackish areas; marginal cell long and narrow hardly wider than second cubital cell, about 0.6 its length from wing tip; third cubital cell wider and much longer than second, nearer margin of wing than the marginal cell, its length on marginal about equal to the length of second on the marginal; basal vein basad of transverse by just about the length of latter; first recurrent vein meets second cubital cell about the middle, the second recurrent meets the third cubital cell before the middle; in rear wings the subdiscoidal is slightly apicad of the origin of cubitus; posterior tibia has 8 or 9 good sized spines on dorsal edge (0.3 to 0.4 as wide as tibiae) surrounded by many hairs about 0.6 as long; claws cleft; the inner ray blunt and very short; longer spur of posterior tibia about one-half as long as metatarsal joint.

Length head and thorax 5.3 mm, abdomen 5.6 mm, fore wing 10.6 mm, rear wing 7.6 mm, length genitalia 1.06 mm, width 0.93 mm, subgenital plate length 1.20 mm, width 0.65 mm.

Subgenital plate with a basal triangular raised area which merges into a low ridge about center of plate and becomes almost evanescent at apex, the raised area bare of hair, rest of plate well haired with prostrate backward directed hair; very much like P. *dakota* but plate not nearly so heavily haired, nor hair as long nor as thick, nor does *dakota* have a row of heavier bristle across basal edge; genitalia similar to *dakota* but again parameres are heavily haired on surface whereas those of *dakota* are bare; the external characters of the adult are much different in the two species. This species is named for my wife Kay, who is an excellent collector. She has added many new species to our collection and even when we collect together she manages to get many species that I do not.

Type Locality.—Tepoztlan, Morelos, Mexico, August 20, 1956, R. R. and K. Dreisbach (*USNM*).

Priocnessus rubrus n. sp.

Holotype female.—Completely light red with the following black markings, dorsal surface of antennae beyond second joint, a streak under the head just behind the mandibles, a streak behind head just in front of neck, which continues and runs around base of fore coxae, the plate just under the tegula, a streak just at base of slope of pronotum, a narrow streak on posterior edge of mesonotum, the anterior margin and sides of scutellum, the metapostnotum and continuing on the suture past the spiracle to middle coxa continuing around rear coxa and across apex of propodeum (a line extending from apex of propodeum to the middle of propodeum which is very broad at apex of propodeum), the under side of thorax and the dorsal side of middle coxae, the base of posterior coxae underneath, and the base of the trochanters more or less; clypeus raised above mouth parts, arched sideways, and slightly concave on front; the clypeus when seen from underneath with just an indication of a tooth in the middle and slightly concave on each side; clypeus just about 2.0 as wide as long; lower interocular distance slightly longer than the upper (16:15); middle interocular distance 0.57 the transfacial; head slightly broader than long; posterior orbits medium, about one-half as wide as eyes; second and third antennal joints about equal to the upper interocular distance; ocelli same size, the laterals 2.5 as far from eyes as each other; ratio of first four antennal joints are as 18:4:24:20; pronotum short on dorsal surface; scutellum about one-third as long as mesonotum, both it and postscutellum raised slightly in middle, convex; metapostnotum about one-half as long as postscutellum, smooth; propodeum short on what might be considered dorsal surface, difference between plane of base and apex more than usual, in a very smooth curve; abdomen widest at apex of second tergite; head and thorax, including propodeum, well haired with fairly long light colored hair, but that on vertex and pronotum dark; abdomen with the last three segments well haired dorsally and ventrally; wings dark over whole surface, glistening in reflected light with a faint purplish sheen; marginal cell long and slender, not wider than the second cubital and 0.6 its distance to wing tip; third cubital cell 1.5 as long as second and 1.5 as long on marginal vein as the second; the third cubital cell extends about as far toward wing tip as marginal cell; a slightly darker cloud in first and second cubital cells, extending slightly into the third cubital and third discoidal cells; the veins of wings dark except the costa and subcostal veins and costal cell, as well as base of both wings are reddish yellow which is very noticeable; the two recurrent veins meet their respective cubital cells at the apical third and before the middle respectively; the basal vein basad of the transverse by the length of the latter; in the rear wing the subdiscoidal vein is apicad of the origin of

cubitus by about 3.5 the thickness of the vein; teeth with broad apex on inner dorsal edge of posterior tibiae, a slightly longer spine just behind each one; on outer edge an exactly similar row of teeth, the space between them slightly grooved and with short hair; these teeth set with the broad surface crosswise to length of tibiae; claws with a small tooth about middle and a pencil of bristles extending from base of claw to outer ray; a few spines under last joint of posterior tarsi.

Length head and thorax 9.3 mm, abdomen 10.0 mm, fore wing 14.7 mm, rear wing 10.6 mm.

Type Locality.—Tepoztlan, Morelos, Mexico, August 20, 1956, R. R. and K. Dreisbach (*USNM*).

Priocnessus aureus n. sp.

Holotype female.—Ground color black and red, with large conspicuous patches of golden and silvery pubescence; mandibles (except base), exposed mentum, apical third of clypeus, slope and dorsal part of pronotum, mesonotum (except side pieces) dorsal surface of scutellum, all dorsal part of abdomen (except basal 0.4 of first tergite), the posterior margins of the first five ventral segments, all of the sixth, and the first five antennal joints, a rather bright red; rest of body black with various patches of silvery and golden shining pubescence; golden, shining, prostrate pubescence on clypeus, face, front to the fore ocellus, posterior orbits, all the pronotum, part of mesonotum and part of scutellum; a large patch of more silvery pubescence on pleura just above middle coxa, at each outer posterior corner of propodeum, and across the base of propodeum; fore coxae and dorsal part of rear coxae also more or less silvery; long somewhat shaggy hair on clypeus, face, head, pronotum, fore coxae, and postscutellum; not so long or shaggy on propodeum, rest of coxae, sides of thorax and apical ventral segments; clypeus concave in front, no tooth and not raised above mouth parts in normal manner; clypeus 2.25 times as broad as long; eyes slightly convergent above, lower interocular distance is 1.15 times the upper; middle interocular distance 0.57 the transfacial distance; head slightly broader than long; lateral ocelli about 1.7 as far from eyes as each other; vertex not higher than eyes, ocelli hardly raised above vertex; ratio of first four antennal joints are as 16:5:29:22; second and third antennal joints just about as long as interocular distance at vertex; posterior orbits slightly more than one-half as wide as eyes; hardly any dorsal surface on pronotum, slightly angulate on posterior edge; mesonotum, almost flat in center, a slight ridge each side running forward from posterior side edge marking off a flange on fore edge as sides expand to pronotal shoulders; scutellum almost half as long as mesonotum, postscutellum more than half as long as scutellum and metapostnotum hardly visible on dorsal surface; propodeum short in a low curve to apex; abdomen widest at apex of second tergite; a very deep transverse groove near base of second ventral, the abdomen much expanded ventrally just beyond it; the fore wing with the fore part of

the whole wing deep brown the rear part (about half on the apical half) transparent as is all the rear wing; marginal cell long and narrow about as wide as second cubital cell; about 0.6 of its length from wing tip; third cubital cell exceptionally long about 1.6 as long as second, extends much beyond marginal cell, only about 0.4 its length from edge of wing, 2.5 as long on marginal cell as the second; the two recurrent veins meet cubital cells about apical fourth and in middle respectively; the basal vein apicad of the transverse in fore wings, less than the length of latter; the subdiscoidal vein in rear wings apicad of cubitus at least four times the width of vein; only one row of the flat, blunt, concave teeth on dorsal surface of posterior tibiae in middle of dorsal surface but divides into two rows about basal fifth; closer together but smaller than in preceding species *P. kayi;* claws toothed with a short tooth before middle and with long slender apical ray.

Length head and thorax 11.2 mm, abdomen 8.6 mm, fore wings 15.2 mm, rear wings 10.6 mm.

Type Locality.—Mexico, No. 2499, C. F. Baker (*USNM*).

Other Localities.—Paratype females: one, La Gloria Cardel, Vera Cruz, Mexico, 1938, J. Camelog, 4408 (*USNM*); one, 8 mi. NE. Taxco, Guerrero, Mex., August 8, 1954, 5150 ft. Univ. Kan. Mex. Exp. (*Univ. Kansas*); No label. Presumably from Mexico (*USNM*); one, Acayucan, Vera Cruz, Mexico, October 22, 1957, R. R. and K. N. Dreisbach (*RRD*).

The last paratype is smaller than the others, its measurements are: length of head and thorax 7.2 mm, abdomen 6.3 mm, fore wing 11.2 mm, rear wing 8.3 mm.

Priocnessus semirufus n. sp.

Holotype female.—Head black with white marks, thorax black with posterior edge of pronotum reddish, abdomen wholly, except base of first tergite and part of second and third ventral segments, black; sides of face, broad inner orbits to lateral ocelli, and a large spot on upper posterior orbits, white; posterior orbits not one-half as wide as eyes; first two antennal joints red, rest black; first three flagellar joints of medium thickness but antennae becoming increasingly slender to apex, the last joint is very slender; coxae black except tips are reddish, trochanters black and red, rest of legs reddish except last one or two tarsal joints are blackish; clypeus raised above mouth parts as usual, the front margin slightly extended in middle and slightly concave on each side; clypeus slightly arched, and sides oblique so that front margin only 0.66 as long as base; clypeus 2.0 as broad as long; middle interocular distance 0.57 of transfacial; lower interocular distance 1.3 upper interocular, eyes converging above; fore ocellus slightly larger, the lateral ocelli 2.7 as far from eyes as each other; ratio of first four joints of antennae 13:4:24:16; second and third joints antennae slightly longer than the upper interocular distance; hardly any dorsal part to pronotum, the posterior edge slightly angulate; scutellum almost one-half as long as mesonotum, postscutellum small not half as long as mesonotum, postscutellum small not half as long as the scutellum;

metapostnotum not much shorter than postscutellum, cross ridged; dorsal part of propodeum almost half length of propodeum, the dorsal part almost level, slope smooth but apex much lower than base, the clypeus, face, pronotum, sides of thorax, propodeum, ventral parts of thorax and under side of coxae with beautiful, golden prostrate, pubescence as well as numerous upright golden hair; long hairs on apex of most of ventral segments of abdomen; abdomen widest about apex of second tergite; dorsal edge of posterior tibiae with a row of teeth on each edge, the ones on inside edge largest; teeth are flat, thin, broad, almost parallel-sided of about eleven in a row, hardly half as long as thickness of tibiae and with a spine behind each one about twice as long; the rows well separated at base but almost come together and disappear before apex; longer spur of posterior tibiae about 0.4 as long as its metatarsal joint; claw with a sharp tooth and sharp apical ray; marginal cell long and narrow, 0.5 of its length from wing tip; third cubital cell very long, twice as long as second, twice as long on cubitus as on marginal; second cubital cell 0.75 as long on cubital vein as on marginal; basal vein much basad of transverse, about the length of latter; the two recurrent veins meet their respective cubital cells at apical third and middle.

Length head and thorax 10.0 mm, abdomen 11.3 mm, fore wing 16.6 mm, rear wings 12.6 mm.

Type Locality.—Huascary, Peru, Sept. 21, 1911, C. H. T. Townsend (*USNM*).

Priocnessus niger n. sp.

Holotype female.—Completely black with only mandibles slightly reddish; wings light yellow with slightly darker apex; clypeus, head, under head, and coxae long thick, almost shaggy haired; thorax, propodeum, apex of abdomen, part of first tergite, and ventral segment not quite so long or shaggy, black haired; clypeus only slightly concave in front, no tooth; rather strongly arched sideways; clypeus not quite twice as broad as long; lower interocular distance slightly more than upper; middle interocular distance 0.58 the transfacial; head slightly wider than long; ocelli the same size, the laterals 2.3 as far from eyes as each other; antennae black, slender and ratio of first four joints are 16:4:26:22; the third joint of antennae is equal to the upper interocular distance; posterior orbits very broad, as wide as eyes; pronotum very short; scutellum large, postscutellum of medium size, metapostnotum almost one-half as long as postscutellum and smooth, no cross wrinkles; propodeum with the dorsal surface slightly longer than usual; abdomen broadest at apex of second tergite, a good groove across second sternite; posterior tibiae with the usual flat teeth subparallel sided with broad blunt tips; the two rows with hardly any space between them, the spines back of the teeth twice as long, the surface of tibiae covered with hairs as long as teeth; marginal cell long and narrow, one-half its distance to wing tip; second cubital cell 1.4 as

long on cubitus as on marginal, receiving first recurrent vein at apical 5/8; third cubital cell 1.5 as long as the second; as long on marginal as the second, receiving second recurrent vein at basal 0.6, it extends well beyond the marginal cell; basal vein in fore wings basad of transverse, slightly more than the length of the latter; subdiscoidal vein in rear wing apicad of cubitus by about thickness of the vein; claws with a broad blunt tooth about middle and a fairly long sharp ray; longer spur of posterior tibia one-third length of metatarsal joint.

Length head and thorax 10.0 mm, abdomen 10.6 mm, length fore wing 14.5 mm, rear wing 11.2 mm.

Type Locality.—Mexico (*USNM*).

Other Localities.—Paratype females: Mexico City, Mexico, September 25, 1957, R. R. and K. N. Dreisbach, (*RRD*), Tepoztlan, Morelos, Mexico, September 26, 1957, R. R. and K. N. Dreisbach (*RRD*). The paratype from Tepoztlan has joints 4-7 of antennae yellowish.

Priocnessus sericeus n. sp.

Holotype female.—Head black with white markings, thorax black, abdomen red, except base of first tergite and ventral segment and a streak across groove on second sternite, which are black; mandibles, except tip and lower edge, sides of face, rather broad anterior orbits to lateral ocelli, and a small spot on posterior orbits just below temples, white; legs with tip of femora and rest of legs except apical tarsal joint (which is black), reddish; antennae with first two joints black, the third black with tip beneath and joints four and five and base of sixth beneath, white, rest of antennae black; ratio of first four joints antennae as 16:4:20:24; the side of clypeus on dorsal surface oblique from eye to apical margin, the side pieces at right angles to surface and this vertical surface concave; the concavity running from eyes around and across front making a slight preapical ridge on clypeus; clypeus slightly concave across apex from the corners; apical edge of clypeus only 0.66 as wide as base; clypeus twice as wide as long; surface of clypeus punctate, shining, slightly longitudinally ridged; lower interocular distance 1.3 times the upper; middle interocular distance 0.57 the transfacial distance; head 1.2 as broad as long; fore ocellus slightly the largest, the laterals 3.0 as far from eyes as from each other; second and third antennal joints equal to the vertex width; vertex at level of eyes, ocellar triangle slightly raised; posterior orbits about 0.5 as wide as eyes; temples very narrow; pronotum very short; mesonotum finely punctate, a slight ridge extending forward from just behind tegula parallel to axis of body forming an angle with the raised side border; scutellum finely punctate; postscutellum about 0.5 as long as scutellum, transversely ridged; metapostnotum about 0.3 as long as postscutellum, and slightly cross-ridged; propodeum with a very short dorsal surface before the smooth slope; abdomen broadest about the apical 0.25 of second tergite; wings almost hyaline but slightly brownish; venation

about as usual; recurrent veins meeting their respective cubital cells at apical 0.33 and basal 0.33; basal vein basad of transverse about length of latter; in rear wings subdiscoidal vein apicad of cubitus by 2.0 thickness of a vein; posterior tibiae as usual with the two rows of teeth with hair between; claws as usual; clypeus, face and all thorax with beautiful, appressed, glistening, silvery pubescence (hence the name); long light colored hairs over, head, thorax, coxae, first tergite, first sternite, last tergite, and more or less over whole sternite.

Length head and thorax 8.6 mm, abdomen 10.0 mm, fore wing 15.2 mm, rear wing 11.2 mm.

Type Locality.—Bogota Colombia, 1931. B. Guevara. (*USNM*).
Other Locality.—Paratype female: Colon, C. F. Baker (*USNM*).

Priocnessus opacus n. sp.

Holotype female.—Body completely black, no marks or color except on antennae; first two joints, basal three-fourths of third and joints 8-12 black, apical quarter of third and 4-7 lemon yellow; the whole thorax opaque, head and abdomen slightly shining; fairly long, thinly placed, hair under head, on coxae and a few on ventral segments; shorter hair on upper part of head, thorax, propodeum, the preceding all blackish, but fairly long dense prostrate ochreous hairs on last tergite; a broad flange in center of front margin of clypeus, the front concave on each side to broad short flanges on the side; clypeus 2.0 broad as wide; lower interocular distance 1.2 the upper; middle interocular distance 0.5 the transfacial; third antennal joint equal to the vertex width; ratio of first four antennal joints is as 14:4:20:14; head 1.2 as broad as long; vertex straight across; hardly any posterior orbits and temples evanescent; occipital carina extends to pregular suture; pronotum very short, postscutellum 0.3 length scutellum and metapostnotum about 0.5 the length of postscutellum, with a few cross ridges; propodeum in a smooth curve to apex; spines on tibiae and tarsi golden, and the tips of tarsal joints are inclined to be reddish; posterior tibiae with exceptionally large teeth on inside edge of dorsal surface, the outer row very close to them and very few hairs between, surface shining; claws as usual, a few spines on under side of last joint; wings yellow with a much darker apex in fore wings, the dark covering the outer half beyond cells, and extending on rear edge to base of third discoidal cell; rear wings with narrower band and not quite so strong but extends around rear of wings to base; third cubital cell extends beyond marginal cell; first recurrent vein meets second cubital cell in *middle,* the second recurrent meets third cubital about basal 0.4; basal vein in fore wing apicad of transverse slightly more than length of the latter; in rear wings subdiscoidal vein is apicad of cubitus by width of vein.

Length of head and thorax 6.7 mm, abdomen 8.0 mm, fore wings 11.9 mm, rear wings 7.6 mm.

Type Locality.—Tepoztlan, Morelos, Mexico, August 20, 1956, R. R. and K. N. Dreisbach (*USNM*).

Priocnessus tricoloratus n. sp.

Holotype female.—Color black, red, and white; head black with base of mandible (0.75 of length), clypeus (except apical edge and black streak in middle), two large spots on anterior orbits between antennae and fore ocellus, spot on posterior orbits just above mandibles, and a spot on upper posterior orbits, white; thorax black with a spot at each outer corner of neck, posterior border of pronotum (except spot in middle) and extending on sides to include tubercle, a large spot in middle of posterior part of mesonotum, a band across scutellum, band across postscutellum, a large elongate spot on mesopleura above middle coxae, an elongate spot under each posterior wing, and a large spot on outer posterior corners of propodeum extending inward along rim, white; abdomen red except base of first tergite, ventral surface and sides of fore coxae, white; fore femora and tibiae black with white streaks; middle coxae reddish and white; middle and posterior femora red; posterior pair of legs all red but last tarsal joint is blackish; middle tibiae and tarsi blackish with some reddish yellow spines; clypeus raised, front almost truncate with a rim; front, vertex and dorsum of thorax finely, smoothly, punctured; fairly long light colored hairs on clypeus, face, under head, coxae, sides of thorax, and propodeum; the fairly long hairs on head and vertex black; long hairs on last tergite reddish; clypeus 2.25 as broad as long; lower interocular distance equal to 1.15 the upper; middle interocular distance 0.5 transfacial; fore ocellus the largest, the laterals 2.0 as far from eyes as each other; head 1.45 as broad as long; anterior orbits very narrow, temples only a line; very short metapostnotum; propodeum in a smooth curve; abdomen broadest about middle of third tergite; posterior tibiae with inner row of teeth on dorsal surface very small, hardly rising above surface but spines of about usual size; outer row with no teeth but spines of same size as other row; only one row at base of tibiae which then divides into the two rows; antennae black except apical half of sixth, seventh, eighth and basal half of ninth are white; ratio of lengths of first four joints are 15:5:20:19; wings hyaline, with faint blackish tip; basal vein basad of transverse by length of latter, which is short; first recurrent meets cell in apical third and the second before the middle; in rear wing subdiscoidal vein is almost interstitial with cubitus.

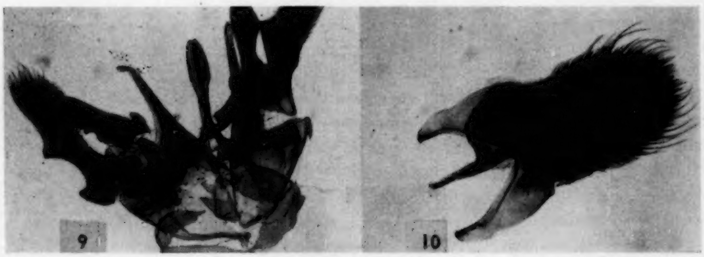
Length of head and thorax 7.3 mm, abdomen 7.9 mm, fore wing 13.5 mm, rear wing 11.2 mm.

Type Locality.—Rio de Janeiro, Brazil, September, 1938, Yel. Fev. Survey M E G. R. C. Shannon (*USNM*).

Other Locality.—Paratype female: Nova Teutonia, Santa Catarina, Brazil, December 21, 1952, Fritz Plaumann (*RRD*).

Priocnessus lineatus n. sp.
Figs. 9, 10.

Holotype male.—Completely black except for a white line on anterior orbits on face; antennae wholly black; antenna has a ridge on



Figs. 9 and 10.—*Priocnessus lineatus* n. sp. 9.—Genitalia (x 30). 10.—Subgenital plate (x 30).

underside (lengthwise) which bears a row of short curved hair, hardly evident on first four and last joints; the head, fore coxae, neck, pronotum, and propodeum with very long, dense, black hair; rest of thorax, last two pair of coxae, first tergite, last three or four tergites, and ventral surface with much shorter black hair; clypeus very much raised above mouth parts and strongly arched; clypeus with three broad teeth, the apical edge concave each side of middle tooth; clypeus 1.6 times as wide as long, the sides oblique from eyes to apical edge, the apical edge 0.6 as wide as base of clypeus, the apical edge as wide as lower interocular distance; the upper interocular distance 1.1 as wide as the lower; the middle interocular distance just about 0.5 the transfacial; head slightly longer than broad, approximately 1.1; ratio of first four joints of antennae as 22:4:16:16; posterior orbits about 0.5 as wide as eyes, temples well evident; ocelli of equal size, laterals 2.0 as far from eyes as from each other; very short pronotum, angulate on posterior border; the sides of mesonotum slightly raised and a line from just behind tegula extending forward parallel to axis of body about half way to anterior edge; scutellum and postscutellum raised on dorsal surface, metapostnotum very evident, smooth and 0.5 as long as postscutellum; propodeum in a very low slope; abdomen widest at apex of third tergite; posterior tibiae with two rows of small teeth and spines, an exact replica of the posterior tibiae of female, but spines and teeth smaller, and two rows closer together; longer spur of posterior tibiae not quite 0.3 length of its metatarsal joint; claws cleft; fore tibiae almost free of spines, middle tibiae well spined; subgenital plate visible as a broad flat basal, hairless plate which narrows about middle of plate, long haired at the sides of this raised area of plate; wings reddish with black tip, extending over outer edge, the rear wings with the tip not so dark but the dark color extends over whole rear of wing; first recurrent vein meets second cubital cell at *middle,* the second meets third cell a little before middle; basal vein basad of transverse by the length of latter; subdiscoidal vein in rear wing apicad of cubitus by width of vein.

Length head and thorax 6.6 mm, abdomen 6.6 mm, fore wings

11.6 mm, rear wings 8.8 mm, length genitalia 1.7 mm, width 1.3 mm, length subgenital plate 1.7 mm, width 0.8 mm.

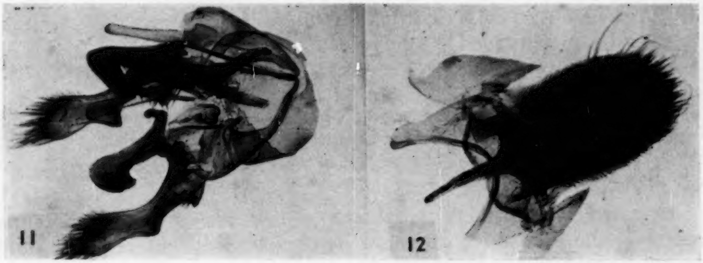
Type Locality.—Rio Blanca, Vera Cruz, Mexico, November 13, 1957, R. R. and K. Dreisbach (*USNM*).

Other Localities.—Paratype males: one, same data as type (*RRD*); five, Tepoztlan, Morelos, Mexico, September 26, 1957, R. R. and K. N. Dreisbach (*RRD*); two, Cuernavaca, Morelos, Mexico, September 28, 1957, R. R. and K. N. Dreisbach (*RRD; MCZ*).

One paratype from Tepoztlan has the apex of fourth antennal joint and the next three antennal joints yellowish, but in every other respect is the same as the rest.

Priocnessus ornamentatus n. sp.

Holotype female.—Body black, much ornamented with yellowish and reddish; front, vertex, head behind, thorax (with large spots more or less all over) and coxae more or less, with beautiful, golden pubescence; long, golden hair on mouth parts, under head, on fore coxae, propodeum, on ventral surface of abdomen, and last tergite; shorter light hair on most of rest of body; mandibles, all but apex, a large spot each side at base of clypeus, broad inner orbits to anterior ocellus, and upper posterior orbits, light yellowish; no marks on thorax; a broad preapical band on first tergite, two broad triangular spots on posterior preapical corners of second tergite, successively smaller spots in similar locations on tergites 3-6, yellow; the posterior edge of first four tergites reddish, and almost all dorsal surface of last two; first four sternites black, mottled with reddish, and last two completely reddish; coxae and trochanters black with apex reddish, rest of legs reddish except last two to four joints of tarsi, blackish with reddish spines; antennae all black with apex of first joint reddish; clypeus arched and raised above mouth parts, a broad very short tooth in center of apical edge, with edge each side of tooth concave on front edge; front edge of clypeus 0.6 as broad as base, the breadth of clypeus slightly more than twice the length; lower interocular distance 1.2 the upper; middle interocular distance 0.5 the transfacial; head 1.15 as broad as long; fore ocellus slightly the largest, the laterals about 2.3 as far from eyes as each other; ratio of first four joints of antennae is 12:4:20:16; the third antennal joint equal to the vertex width; posterior orbits about 0.67 as wide as eyes; hardly any temples; vertex straight across from eyes, ocellar triangle slightly higher; pronotum very short; mesonotum short, twice as long as scutellum, postscutellum one-half as long as scutellum, metapostnotum almost 0.6 as long as postscutellum, with a few cross ridges; propodeal slope in a smooth curve; posterior tibiae as usual except very short distance between the two rows of teeth and those on outer edge are very short and narrow; longer spur of posterior tibia 0.4 length of the basitarsus; claws as usual; first recurrent vein meets second cubital cell at apical third and the second recurrent meets third cubital at basal third; the basal vein is basad of transverse vein,



Figs. 11 and 12.—*Priocnessus prominens* Banks. 11.—Genitalia (x 15). 12.—Subgenital plate (x 15).

1.5 the length of transverse vein; in rear wings the subdiscoidal is interstitial with the cubitus; wings yellowish hyaline, veins yellow.

Length head and thorax 7.3 mm, abdomen 6.4 mm, fore wings 10.6 mm, rear wings 8.6 mm.

Type Locality.—Cerro Verde, El Salvador, September 11, 1956, 714-29, P.A.B. (*USNM*).

Priocnessus prominens Banks
Figs. 11, 12.

Male.—Head black, with base and upper edge of mandibles, mentum, clypeus (except a small basal spot) face (except a continuation of black of clypeus) broad inner orbits to lateral ocelli, a spot on upper posterior orbits, whitish; thorax black with neck whitish and tegula reddish; thorax covered all over with brilliant patches of beautiful prostrate golden pubescence; abdomen deep red except base of first tergite (both ventrally and dorsally) is black, and apical half of ventral part is blackish; first two joints of antennae completely red, rest of antennae black on top, brown underneath; joints of antennae long and slender, slightly hollowed in center; coxae blackish more or less on base and dorsal surface, reddish on ventral surface; rest of legs red except last one or two tarsal joints are black; a very strong rather sharp tooth on apex of under side of last trochanter; under side of head, fore coxae and propodeum with long, golden hair, the rest of head and thorax, first tergite and apex of abdomen with considerable, much shorter, hair; clypeus very much arched, and raised above mouth parts, deeply concave on apex with a small broad tooth in middle; clypeus 2.5 as broad as long, front edge 0.6 as wide as base; lower interocular distance 1.25 as long as upper; the middle interocular distance 0.56 as long as transfacial; fore ocellus the largest, the laterals 2.0 as far from eyes as each other; ratio of length of first four antennal joints is as 12:5:20: 19; the second and third joints about as long as vertex width; metapostnotum about 0.3 as long as postscutellum; wings yellowish hyaline; both recurrent veins meet their respective cells at basal third; the basal

vein in fore wings basad of transverse vein by more than length of latter; in rear wings subdiscoidal vein is interstitial with the cubitus; posterior tibiae has small teeth and spines three times as long with long hair between.

Before dissection the subgenital plate shows a hairless raised surface triangular in shape at base as broad as visible part and extending the length of plate, triangle not closed at apex; plate rectangular and with spines around sides and apex, those on apical half and around the broad, blunt apex the longest; genitalia characteristic; the parameres with apical half broad and blunt, the basal half with a very deep concavity on inside.

Length head and thorax 7.4 mm, abdomen 6.0 mm, fore wing 12.0 mm, rear wing 10.0 mm, length genitalia 1.4 mm, width, 0.53 mm, subgenital length 1.59 mm, width 0.66 mm.

Range.—Peru, Colombia.

Priocnessus caesius n. sp.

Holotype female.—Head and thorax with ground color bluish-gray (hence name), abdomen completely red; two spots on basal outside corners of clypeus, interior orbits to fore ocellus, a spot on temples back of eyes, reddish; pronotum appearing a deep red, the posterior margin transverse; the head and thorax covered with a fine pubescence, very strongly silvery on sides of propodeum; propodeum very short; coxae and trochanters black, suffused with reddish, rest of legs red; clypeus well arched and above mouth parts, a rim on front edge; front edge slightly concave; basal width of clypeus 1.60 width of apex, 1.9 as broad as long; lower interocular distance about 1.3 the upper; middle interocular distance is approximately 0.5 the transfacial; fore ocellus much the largest, the laterals 2.0 as far from eyes as each other; apex of third joint and forth and fifth joints bright yellow, rest black; ratio of first four joints of antennae is 15:4:24:20; the third joint of antennae slightly longer than vertex width; wings light yellowish, subhyaline; first recurrent meets second cubital cell beyond apical third and the second meets third cubital about basal third; in fore wings basal vein basad of transverse the length of the latter; in rear wings the subdiscoidal apicad of cubitus the width of a vein.

Length head and thorax 7.9 mm, abdomen 6.5 mm, fore wing 13.2 mm, rear wing 10.2 mm.

Type Locality.—Ecuador, C. F. Baker (*USNM*).

Priocnessus anomalus n. sp.

Holotype female.—Head and thorax black, with yellowish and reddish markings, abdomen rufous with yellow markings; mandibles (except base), clypeus, visible part of mentum, inner orbits to above antennae, and a small streak in upper posterior orbits, reddish yellow; posterior edge of pronotum and lower edge, a small spot in

middle of posterior part of mesonotum, most of scutellum, center of postscutellum, and a small streak across dorsal part of propodeum, reddish and yellow; abdomen with base of first tergite black and yellow, and a spot on sides of second tergite yellow; ventral part of abdomen black suffused with reddish; antennae with the first six joints red, the last six black; clypeus hardly raised above mouth parts, the front margin slightly wavy and only slightly projecting under eye; vertex slightly arched above eyes, the ocellar triangle slightly higher; upper and lower interocular distance the same; middle interocular distance is 0.5 the interfacial; fore ocellus slightly larger and laterals 2.0 as far from eyes as from each other; clypeus slightly more than 2.0 times as broad as long; head about as broad as long; ratio of first four antennal joints is as 14:4:30:25; third antennal joint slightly longer than vertex width; pronotum short, very slightly angulate behind; scutellum and postscutellum both raised in center, slightly cone-shaped; metapostnotum very broad, 0.7 as long as postscutellum, slightly wrinkled; propodeum very low; posterior tibiae with the teeth on inner edge very broad at base and becoming smaller and almost fading out before apex, the teeth concave in front and yellow with the inner edge reddish; coxae, trochanters and base of femora to one-half of femora, and rest of legs reddish, including all of tarsal joints; wings slightly like those of *aureus,* the fore half of fore wings deeper yellowish than the rear half and the rear wings; the basal vein basad of transverse by *less* than the length of the latter; in rear wing the subdiscoidal vein apicad of the cubitus by 4 or 5 times the width of vein; first recurrent vein meets second cubital cell at apical third and second recurrent meets third cubital at basal fourth; head, postscutellum, and propodeum fairly well haired with golden hair, rest of body with much shorter and much less hair.

Length head and thorax 8.6 mm, abdomen 9.9 mm, fore wing 15.6 mm, rear wing 11.1 mm.

Type Locality.—Guadalajara, Mexico, September 17, 1957, R. R. and K. N. Dreisbach (*USNM*).

This species has several characteristics slightly different than most species of the genus. The clypeus is hardly raised above mouth, the eyes are rather strongly emarginate just above base of antennae, the sides of clypeus hardly extend under eyes, the scutellum and postscutellum are much raised above surface of mesonotum (especially the postscutellum is almost cone-shaped), the teeth on inner edge of dorsal surface of posterior tibiae are very strong (and strongly concave on front) at base and become successively shorter and fade out before apex, the basal vein in fore wings is basad of transverse vein by a smaller distance than the length of the transverse, in rear wings the subdiscoidal vein is a greater distance apicad of the cubitus than is usual (about 5 times the width of a vein) in the species from Mexico and southward; the U. S. species have this vein apicad of cubitus a greater distance.

Priocnessus hurdi n. sp.

Holotype female.—Completely rufous except for the following black markings: apical third of mandibles, the dorsal part of thorax just back of attachment of fore wings back to and including a streak across base of propodeum, the latter extending downward on sides to the suture, the side of thorax below pronotum and the whole ventral surface of thorax including ventral surface of coxae and the transverse groove on second ventral segment; the first two and base of third antennal joints red above and below; the rest of antennae below reddish, the dorsal surface black; wings trifasciate with a black band across basal veins from subcosta to rear of wing, a second black band from basal third of marginal cell back to rear edge of wing, expanding in width to rear where it continues backward along rear edge to meet the black band across apex; wings yellowish, not clear, the veins reddish yellow except in dark areas, the stigma also reddish yellow; rather long, scant black hair on front, vertex and on dorsum of scutellum and postscutellum, hair on rest of body yellow; front margin of clypeus produced at corners, and less in the middle with edge slightly concave each side of center; clypeus 2.0 as broad as long; eyes slightly converging above, upper interocular distance is 26, lower 30 (on same scale as antennal measurements) ratio of lengths of third and fourth antennal joints is 20:18; head about 1.1 as broad as long; ocelli 2.0 as far from eyes as each other; the teeth on inner edge of posterior tibiae (the larger row of teeth) with the outer edge (about 0.3 of width) darker, this dark stripe extending across apex and a short distance on inner edge.

Length head and thorax 7.3 mm, abdomen 8.0 mm, fore wing 13.2 mm, rear wing 9.20 mm.

Type Locality.—10 km. W. of Zetacuaro, Michoacan, Mexico, July 11, 1951. P. D. Hurd (*USNM*).

Other Localities.—Paratypes (8): two, same data as type (*Hurd; MCZ*); two, Alpuyeca, Morelos, Mexico, July 3, 1951, Hurd (*Hurd; RRD*); one, Alpuyeca, Morelos, Mexico, June 27, 1951, Hurd (*Hurd*); one, 15 km. E. Sombrereta, Zac., Mexico, July 28-31, 1951, Hurd (*RRD*); one, Ahuacatlan, Nyarit, Mexico, July 18, 1951, Hurd (*Hurd*); one, 16 mi. S. of Cuernavaca, Morelos, Mexico, Aug. 22, 1958, H. Howden (*Howden*).

A few of the paratypes have more black on the dorsum of thorax, the color of antennae also varies. In some specimens the first one or two joints of antennae are red, above and below, the third, fourth and basal half of fifth are black, the apical half of fifth, the sixth and basal half of seventh white, the rest of antennae black. The bands on wings also vary, some not so black or covering less area. Otherwise they are uniform.

The paratype from Ahuacatlan was pinned on the same pin with an immature female spider of the genus *Euagrus* determined by Gertsch. This record was discussed in the literature by P. D. Hurd, Jr. and Marius S. Wasbauer (1956, *Jour. Kan. Ent. Soc.*, 29(4):169).

Priocnessus durangoensis n. sp.

Holotype female.—Head all black except a preapical reddish mark on mandibles, and a yellowish short, narrow, mark on interior orbits from antennae to fore ocellus; thorax, coxae and trochanters completely black; abdomen completely rufous except black at extreme base; basal 0.75 of fore femora black, and base of last two pair femora black, rest of legs completely rufous; apex of third joint of antennae, the fourth, fifth, and basal third of sixth joint white, rest of antennae black; clypeus slightly produced on outer front edges, the middle also slightly produced, thus with a slight concavity each side of middle; a narrow, shining, hairless rim on front edge of clypeus; clypeus 3.0 as broad as long; upper interocular distance (23) slightly less than the lower (26); ratio of lengths of third and fourth antennal joints is 22:18; head 1.2 as broad as long; lateral ocelli 2.5 as far from eyes as each other; silvery pubescence on head and thorax; considerable long white hair under head, dorsal surface of head and propodeum; wings hyaline, slightly dusky (yellowish), veins and stigma yellowish; basal vein in fore wing basad of the transverse by 1.5 the length of transverse; in the rear wings the subdiscoidal vein is apicad of cubital vein by just about the width of a vein; fore femora with a few long hairs on under side.

Length of head and thorax 6.6 mm, abdomen 7.8 mm, fore wings 11.5 mm, rear wings 9.6 mm.

Type Locality.—El Salto, Durango, Mexico, Aug. 3, 1951, P. D. Hurd (*USNM*).

KEYS TO SPECIES OF NEOTROPICAL PRIOCNESSUS

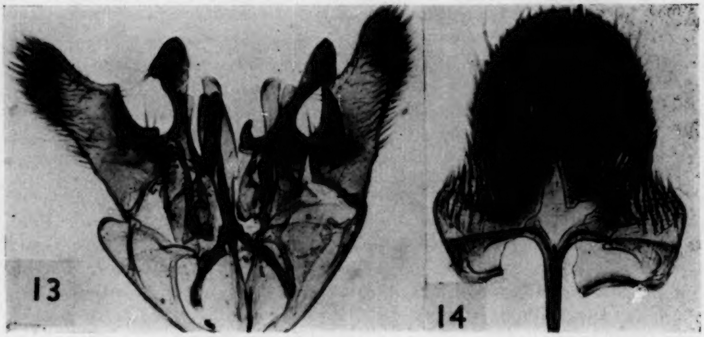
KEY TO MALES

1. Clypeus yellow, with a large black spot in middle, anterior orbits broadly yellow; mandibles largely yellow, tip and generally lower edge black; abdomen black, marked with rufous or yellowish or wholly rufous; wings hyaline or slightly yellowish, wings not banded, tips of wings *not* black; antennae black or black on dorsal surface, dark brown on under side, or in one case black with third and fourth joints yellow 2

1. Clypeus with no yellow marks whatever; in one case very narrow anterior orbits yellow; mandibles all black; abdomen black; wings strongly yellowish with black tip and in one case slightly banded; antennae black or some of middle joints yellow 5

2. Last trochanter with a strong tooth on apex of under side *and* abdomen red, legs red (including under side of coxae) except last two or three tarsal joints which are black; first two joints of antennae red, the rest black; head and thorax with golden prostrate pubescence spotted over most of surface; wings rather strongly fumous, yellowish; subgenital plate somewhat elevated, rectangular, with spines over apical sides and across apex. Peru and Colombia, (Figs. 11, 12) ....*prominens* Banks

2. Last trochanter with no tooth or with only an indication of one; abdomen black with yellowish spots or fuscous with yellowish spots; basal two joints of antennae black, rest of antennae black or brown on underside; head and thorax adorned with golden, silvery or no pile; wings almost



Figs. 13 and 14.—*Priocnessus apache* (Banks). 13—Genitalia (x 45). 14.—Subgenital plate (x 45).

hyaline with yellow veins or flavo-hyaline with testaceous veins; subgenital plate either similar to preceding or not rectangular but with sides concave near center 3

3. Wings with cloud over basal and transverse veins, from base of marginal cell backward over second cubital cell, and over apical half of third discoidal cell, and apex of wing beyond cells black; wings dark yellowish, costal vein *yellow*, rest of veins dark; clypeus, posterior orbits, all of pronotum, mesonotum, scutellum, and abdomen, red; legs also red. U.S. and Mexico. (Figs 13, 14.) .... *apache* (Banks)

3. No cloud whatever in wings; costal vein *not yellow* with rest of veins dark; body without the parts listed above all red 4

4. Pubescence of head and thorax without the least tinge of golden only slightly silvery *and* a few very small maculations on thorax; two narrow preapical lines on pronotum, large spot on scutellum, a faint mark each side just above middle and posterior coxae, yellow; abdomen black with a mark on middle of dorsal surface of first tergite, one on each side just before apex on first tergite, a large spot each side on second, third, and fourth tergites, yellow; legs *black* with the knees of femora and a stripe on posterior edge of tarsi yellow; antennae brown beneath, black above; wings hyaline; no tooth on posterior trochanter. Mexico. (Figs. 3, 4.) .... *octomaculatus* n. sp.

4. Pubescence of the head and thorax golden or strongly silvery with a trace of golden; no maculations whatever on thorax; abdomen blackish with maculations more numerous and reddish or fuscous with yellow marks; legs ferruginous; there may be an indication of a small tooth on posterior trochanter; antennae reddish on under side, dorsal surface blackish, *and* the last three joints much enlarged and flattened, whitish mottled with black; first tergite with yellow and reddish markings just before apex, two reddish spots on sides of second and third tergites, the posterior border of all tergites 2-6 reddish, the seventh tergite wholly reddish; subgenital plate rectangular with a raised hairless area over most of surface. Costa Rica. (Figs. 5, 6.) .... *orbiculatus* (Smith)

5. Narrow yellow lines on anterior orbits from base of clypeus or just above; clypeus with three teeth on front margin, middle one small triangular,

the sides concave each to the lateral broader teeth; clypeus much raised above mouth parts, strongly arched 6

5. No marking on anterior orbits, body wholly black; clypeus *without* teeth concave on front margin or almost truncate 8

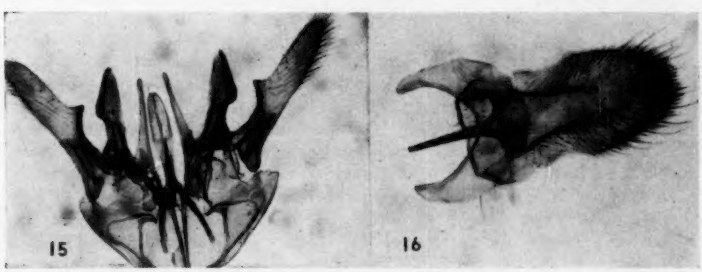
6. Antennae wholly black; wings reddish with contrasting black tip; subgenital plate elongate, gradually narrowing from base to broad obtuse apex; a few long hairs almost as long as width of plate on sides near apex and around apex; a raised hairless area, broad at base then gradually converging to apical fourth, sides above base subparallel; parameres of genitalia with a large concavity on outside near base. Mexico. (Figs. 9, 10.) .... *lineatus* n. sp.

6. Antennae with some joints completely yellow; wings reddish with a black cloud in second cubital and third discoidal cells, or hyaline with black veins; subgenital plate shorter and ovate, or as long but sides concave just above base 7

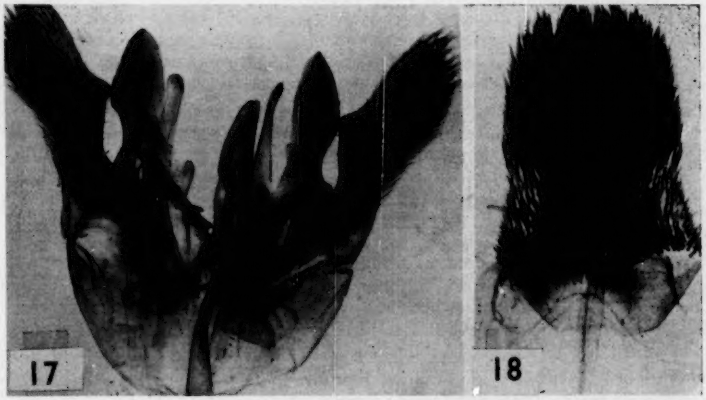
7. Antennal joints 5-8 completely yellow, joints 3, 4 and 9-11 yellow beneath, black on dorsal surface; linear impressions on joints 6-8; wings reddish yellow with a blackish cloud in second cubital and third discoidal cell; apex of wing blacker than in *lineatus* covering most of surface beyond the cells and extending around rear of wing to base of third discoidal cell; subgenital plate much shorter than in *lineatus*, ovate, triangular area shorter, not as broad; shorter hair on sides and around apex; parameres of genitalia short and broad, the outside edge straight without a large concavity. Mexico. (Figs. 7, 8.) .... *kayi* n. sp.

7. Some of middle antennal joints yellow; wings hyaline with dark veins; subgenital elongate, with the sides just above base concave, a broad basal triangle which is open at apex, the prominent sides of triangle ending about middle of plate; parameres of genitalia much more slender and longer than in *kayi*. Panama. (Figs. 15, 16.) .... *neotropicalis* (Cameron)

8. Head and thorax with hair black, only slightly reddish in reflected light, no appressed reddish pubescence; clypeus hardly raised above mouth parts and truncate in front; eyes reach vertex; pronotum transverse behind; subdiscoidal vein of rear wing is interstitial with the cubitus; no teeth and only a very few small spines on posterior tibiae; subgenital plate concave on sides about middle, the upper half of plate semiorbicular, the raised portion at base wider than in next; smaller size about 13 mm long. Honduras. (Figs. 1, 2.) .... *hondurensis* n. sp.



Figs. 15 and 16.—*Priocnessus neotropicalis* (Cameron). 15.—Genitalia (x 30). 16.—Subgenital plate (x 30).



Figs. 17 and 18.—*Priocnessus rogersi* Dreisbach. 17.—Genitalia (x 30). 18.—Subgenital plate (x 30).

8. Head and thorax with reddish black hair and with appressed reddish pubescence; clypeus raised above mouth parts and concave on front margin; pronotum angulate behind; subdiscoidal vein in rear wings apicad of cubitus; small teeth and spines on dorsal surface of posterior tibiae; subgenital plate almost rectangular, only slightly concave on sides near middle, the upper half with sides parallel to close to apex; size larger, about 15 mm. Mexico. (Figs. 17, 18.) ....*rogersi* Dreisbach

KEY TO FEMALES

1. White or yellow maculations on the thorax (*not* glittering spots of pubescence), head also well maculated, abdomen black with a great deal of yellow or completely rufous; wings white hyaline or slightly to strongly yellowish hyaline 2
1. No maculations on thorax but patches of silvery or golden pubescence may seem like maculations; wings generally strongly fuscous yellowish or reddish, in only about two species are wings yellowish hyaline 4
2. Clypeus with a small broad tooth on middle margin, margin each side concave; abdomen black, most of dorsal surface of first tergite yellow, two very large spots on sides of second tergite and two smaller ones on sides of third tergite, reddish yellow; first three joints antennae reddish, the rest black above, brown beneath; mandibles (except black apex), all clypeus, all face, front and broad anterior orbits to vertex, yellowish white, except a black streak in middle of front; posterior orbits all yellowish white; most of pronotum, a broad spot on mesonotum, band across scutellum middle and posterior edge of postscutellum, a large spot above middle coxae, smaller one under rear wing, the outer posterior corners of propodeum, and a spot above rear coxae, yellowish white. Costa Rica ....*flavidus* n. sp.
2. Clypeus almost truncate in front; abdomen almost completely rufous on dorsal surface, base of first tergite is black and may have a yellow

spot on base of first and sides of second tergite; rather broad anterior orbits, a spot on upper posterior orbits, a spot on posterior middle of *mesonotum,* dorsal surface of scutellum, and postscutellum, yellow or yellow with some reddish 3

3. Antennae with first five and one-half joints and last three and one-half joints black, joints in between yellow; mandibles except apex, clypeus except black spot in middle), posterior edge of pronotum (except in middle) extending downward and covering tubercle, a large spot just above middle coxae, a large spot under rear wing, a large spot on outer posterior corners of propodeum continuing on outer corner of rim, and ventral surface of fore and middle coxae, white; fore tibiae black and white, posterior femora and tibiae red; fore tarsi, middle tibiae and tarsi and last joint of posterior femora and tibiae, red; fore tarsi, middle tibiae and tarsi and last joint of posterior tarsi black; ventral surface of abdomen reddish suffused with black; wings almost hyaline. Brazil ....*tricoloratus* n. sp.

3. Antennae with first seven joints reddish (dorsal surface blackish), the rest black; mandibles (except base and apex), all of clypeus, lower side edge of pronotum, and legs beyond femora, reddish; broad posterior border of pronotum yellow with a reddish front edge; coxae, trochanters, and about basal half of femora black; abdomen with base of first tergite black and yellow and a yellow spot each side of second tergite; ventral surface of abdomen black with second and third ventrites suffused with yellow; wings with fore half of fore wing deep yellowish brown, the rear half and rear wing much lighter colored. Mexico ....*anomalus* n. sp.

4. Face and front densely bright golden pubescent, also some golden pubescence on thorax and abdomen 5

4. Face and front and abdomen without any golden pubescence; thorax may have slightly golden pubescence, if so the antennae is yellow beneath and posterior orbits have a yellowish band 6

5. Face and front, densely golden pubescent, some on thorax but none on abdomen; posterior three-fourths of pronotum a deep red, with silvery pubescence which appears slightly golden in reflected light; mesonotum and scutellum a deep red with no pubescence; a broad spot above middle coxae, the outer posterior corners of propodeum and the anterior corners of propodeum with brilliant shining silvery (slightly golden) appressed pubescence; the fore part of fore wing back to rear edge of second discoidal cell and covering cubital cells and fore edge of third discoidal and extending to wing tip, a deep brown, the rear of wing and all of rear wing hyaline; the comparison very prominent; exposed part of mentum and fore edge of clypeus red, the latter not much raised above mouth and concave on fore margin; abdomen red, legs black to about middle of femora then reddish; first five joints antennae reddish, last seven black. Mexico ....*aureus* n. sp.

5. Face, head, and thorax densely covered with golden pile and with long pale fulvous hair; head and thorax black; coxae and trochanters black; pronotum black, as is rest of thorax; no large noticeable pubescent spots on thorax; the wings unicolorous; antennae entirely black; clypeus broadly yellow laterally, no yellow on posterior orbits; anterior portion of three or four basal abdominal segments more or less black with short golden pile on apical tergite, the second to fifth segments with a short golden pile at the apex. Panama, Mexico ....*orbiculatus* (Smith)

6. Insect completely rufous except for sternum of thorax, tips of mandibles, some sutures on thorax and base of first tergite, are black, *and* wings deep fuliginous or banded; or body completely rufous with black as above *and* wings light yellow and banded; pronotum angulate behind 7

6. Insect not completely rufous and wings not fuliginous or banded 9

7. Insect rufous as in first part of couplet 4 *and* with deeply fuliginous wings; clypeus much raised above mouth parts, an indication of a tooth in front margin and concave each side of it; first two joints of antennae reddish, last 11 joints yellowish underneath, black on dorsal surface; first recurrent vein received by second cubital cell at apical third. Mexico .... *rubrus* n. sp.

7. Wings banded, with a dark band over basal veins, one over base of marginal cell and backward to rear of wing, and one on apex of wing beyond third cubital cell; wings yellowish between the bands 8

8. Insect rufous all over; only with very little black color on dorsal part of base of propodeum; no hairs on femora and no hairs on head or dorsum of thorax; head slightly longer than broad (42:40); clypeus about 2.3 as broad as long; ratio of lengths of third and fourth antennal joints is 18:16; upper interocular distance slightly less than lower (20:22); a broad dark band over basal and transverse veins, a second one from base of marginal cell through all of second cubital and base of third cubital and across apical three-fourths of third discoidal cell; clypeus hardly raised, truncate and with a slight rim; first two joints antennae reddish, rest brown beneath and black above; first recurrent vein received by second cubital cell just before middle. U.S. and Mexico .... *apache* Banks

8. Insect not rufous all over, at least ventral surface of thorax black; head broader than long; ratios of various measurements different than in *apache;* apex of propodeum as well as sutures on side of thorax black, more black on base of propodeum; black upright hair on front, vertex and dorsal surface of scutellum and postscutellum, hair on rest of body yellow; first two joints of antennae red above and below, rest of dorsal surface deep black or with the fifth and sixth joints yellow. Mexico .... *hurdi* n. sp.

9. Body all black, at most with a slight reddish streak on anterior orbits; wings light yellow. 10

9. Body not all black, either with maculations or some red color; wings generally more hyaline 14

10. Antennae, except tips, legs, and tip of abdomen fulvous; body fusco-ferruginous; wings yellowish hyaline; apex of fore wings fuscous and a cloud between the middle and apex fuscous. Cuba .... *nubeculatus* (Cresson)

10. Antennae wholly black, or with basal joints to four or six yellowish and rest of antennae black; no band in fore wings 11

11. A reddish streak on anterior orbits; very hairy on head and thorax, and long hair beneath fore femora, some on mid femora above; first joint of antennae long haired; subdiscoidal vein in rear wing much apicad of cubitus; antennae black; pronotum angulate behind. Mexico .... *rogersi* Dreisbach

11. No marks on anterior orbits; not quite so hairy, less hair or none on

face and middle femora; no long hair on first antennal joint; subdiscoidal vein in rear wing only slightly apicad of cubitus; antennae black or partly yellow; pronotum transverse behind 12

12. Antennae black to apical fourth of third joint, yellow from there to apex joint 7, then black to apex; a broad flange (wide tooth) in middle of front margin of clypeus, slightly concave each side, a narrow rim on clypeus; thorax almost free of hair, only a very few short hairs under fore femora; third antennal joint 1.2 as long as fourth; posterior tibiae with very broad teeth on inner margin, very small ones on the outer margin; glistening between the teeth. Mexico ....*opacus* n. sp.

12. Antennae wholly black or with joints 4-6 yellow; no tooth on front of clypeus 13

13. Antennae wholly black or with joints 4-6 yellow; clypeus slightly concave across front, a rim on front edge of clypeus; thorax very hairy; fore and middle femora more hairy; third antennal joint 1.1 as long as fourth; although this species is larger than preceding, the teeth on inner margin of posterior tibiae only about 0.5 as broad and opaque between teeth. Mexico ....*niger* n. sp.

13. Antennae wholly black, pruinose; clypeus and face below antennae densely covered with a silvery pile; clypeus elongate, obliquely narrowed toward apex, which is subtransverse; mandibles elongate, shining, apex piceous; two round spots of silvery pubescence at apex of propodeum; abdomen shining, pruinose, apical segment thickly clothed with blackish hairs, those at apex being rufous; wings hyaline, broadly violaceous at apex. Guatemala ....*guatemalensis* (Cameron)

14. Head and thorax with golden pubescence; head black with yellow maculations, thorax black (neck may have yellow streak) with only the yellow, appressed pile; abdomen ferruginous or black with yellow and reddish maculations; wings flavo-hyaline, veins yellowish 15

14. Head and thorax without golden pile, thorax and abdomen different 18

15. Abdomen black, maculated as follows: two preapical spots on sides of first tergite, a large spot each side in middle of second tergite, two smaller linear spots on sides of third tergite, two spots about same size on sides of fourth tergite, yellow; the apex of first four tergites rufous and the last two tergites as well as last two sternites completely rufous; the first four sternites with posterior edges rufous; most of mandibles, a large spot each side of clypeus, face, broad anterior orbits, a spot in upper posterior orbits and narrow line on neck, yellow; antennae entirely black; coxae and trochanters black; rest of legs reddish except last joint fore tarsi, last three joints middle tarsi, and last four joints of posterior tarsi black or blackish; clypeus with a small tooth in middle, slightly concave each side, a narrow rim on apex; large teeth on posterior tarsi. Costa Rica ....*ornamentatus* n. sp.

15. Abdomen ferruginous; coxae black, most of rest of legs reddish 16

16. A spot each side of clypeus yellow; basal margins of abdominal segments fuscous; third and fourth joints of flagellum yellowish, rest black; wings flavo-hyaline, nervures testaceous; a small species about 12 mm; spines back of teeth on posterior tibiae not twice as long as teeth. Mexico, El Salvador ....*orbiculatus* (Smith)

16. Clypeus completely black; basal margins of abdominal segments not fuscous, completely red; the spines just back of teeth on dorsal edge of posterior tibiae (on both inside and outside edge) twice as long as teeth 17

17. Antennae with the first two joints and base of third red, rest black; wings a strong reddish yellow, veins strongly reddish except subcosta is amber from base to slightly beyond basal vein; sides of face yellowish from base of antennae to eyes, the yellow color continuing on anterior orbits to the fore ocellus, almost as broad on front as on face; mandibles yellowish on basal half black on apical half; in certain light pubescence on face and thorax golden; apex of fore coxae yellow, all trochanters red; legs all red except the two apical tarsal joints; a large species 21.5 mm long. Peru ....*semirufus* n. sp.

17. First two and three-fourths of third antennal joints black, apex of third, the fourth, fifth and basal three-fourths of sixth white, rest black; wings hyaline, slightly dusky, veins yellowish in reflected light; face black, anterior orbits from antennae to just before antennae with a whitish line; basal 0.75 of mandibles black, a preapical red streak, the apex black; head and thorax completely black with silvery pubescence; all coxae and trochanters black; basal half of fore femora black, and base of last two pair black, rest of legs all reddish including apical tarsal joints; a smaller species, 13.4 mm. Mexico ....*durangoensis* n. sp.

18. Head, thorax and abdomen mostly black with white or yellow maculations 19

18. The whole body yellowish or at least the abdomen rufous 20

19. The sixth antennal joint entirely, the fourth broadly at apex, and the fifth at base, yellow, the rest of antennae black; mandibles (except at apex), clypeus broadly at side, inner orbits broadly, the outer orbits more narrowly at top and bottom, the edges of pronotum all around (except in middle in front) tegula, a mark in center of mesonotum, middle of scutellum, a mark on post scutellum, two marks on mesopleura behind (the lower one the longer), a mark on lower and anterior end of metapleura, and a large mark on sides of abdominal tergites, yellow; a tooth in middle of front edge of clypeus; ventral surface obscure yellow; wings hyaline, nerves black; head and thorax opaque. Panama ....*neotropicalis* (Cameron)

19. Antennae completely black; mandibles black, clypeus black; anterior orbits narrowly, a spot back of eye on temple, a small spot on anterior corners of neck, preapical posterior border of pronotum (except in center), a spot on posterior center of mesonotum, a band on scutellum, a small spot under posterior wing, a larger spot above middle coxae, a spot on outer posterior corners of propodeum, spots on extreme sides of first four tergites, yellow; legs black, but middle and posterior tibiae yellowish on posterior edge, and some on sides, these parts and tarsi with golden colored spines; a tooth on fore margin of clypeus; head and thorax (particularly thorax) shining, fore part of pronotum and neck bare and shining. Mexico ....*octomaculatus* n. sp.

20. Whole body pale yellowish, pronotum angulate behind 21

20. Head and thorax black or black and maculated, abdomen rufous 22

21. Antennae pale on first and second joints, black beyond; head, thorax and abdomen reddish yellow, legs and palpi also, but tarsi darker; fore wings rather yellowish in the cells, veins dark and bordered with dark or smoky, broadly so at basal vein and a broad dark cloud over most of marginal cell and back into apical part of third discoidal cell, wing tip smoky, hind wing also yellowish, tip smoky; head, thorax, coxae, venter and three apical segments with rather long fine hair; some

appressed golden hair on head; both recurrent veins meet their cell at about middle. West Indies .... *monticolus* (Banks)

21. Antennae mostly pale yellowish, but last six joints pale brown; a dark stripe above antennae each side reaching up to ocelli; a narrow black line from eye to eye; mesonotum with a broad median black mark, not reaching hind border, each side a broad black stripe from wing base forward and connected to each other behind, thus leaving a pale U in middle; scutellum with a black spot in middle of base, black behind, postscutellum yellowish across frontal part; propodeum with a large black streak each side leaving only a narrow pale median line, the dark sides narrower behind; pleura entirely pale; wings mostly hyaline, fore wings with a pale brown costal streak beyond basal vein and covering marginal, first, second, and most of third cubital cells and beyond to wing tip. Colombia .... *bequaerti* (Banks)

22. Head and thorax with pale yellow or creamy white spots; clypeus, a broad streak on anterior orbits not touching clypeus, a streak on posterior orbits, an elongate spot on each side of hind margin of pronotum and the lower margin broadly and almost touching side spot of hind margin, a median spot behind on mesonotum, a small spot on scutellum, a larger one on postscutellum; one on outer side of fore coxae and several on sides of thorax, pale yellow or creamy white; petiole of abdomen and fore femora black except rufous on tip; mid and hind femora, all of tibiae, and basal part of tarsi pale yellowish, last few tarsal joints jet black; antennae with six or six and one-half joints jet black, five or four and one-half creamy-white, the last joint brown; pronotum angulate behind. Trinidad .... *ornatus* (Banks)

22. Thorax not maculated and otherwise not as above 23

23. Coxae, trochanter and femora, except apex, black; apex of femora and rest of legs reddish, except last two tarsal joints of fore legs and last three tarsal joints of middle and posterior legs, black; head and particularly the thorax strongly silvery, sericeous with prostrate, glistening pubescence; clypeus slightly concave in front, with a rather broad, preapical rim, which forms a slight trough (concave), particularly on the side pieces; mandibles (except tip and lower edges), sides of face, rather broad anterior orbits to lateral ocelli, and a small spot on posterior orbits just below temples, white; antennae with first two and basal three-fourths of third joints black, apex of third and joints four and five, and base of six underneath, white; third joint of antennae not as long as fourth; lower interocular distance 1.3 times the upper; thorax especially shaggy, long haired, hairs light colored. Panama, Colombia .... *sericeus* n. sp.

23. Legs all red, except coxae and trochanter are mostly black, and last tarsal joints blackish; body not silvery sericeous; clypeus with an indication of a broad tooth in middle of front and slightly concave each side, a preapical rim on anterior edge of clypeus; thorax slightly silvery, slightly bluish; first two joints antennae black, apex of third and all of fourth and fifth bright yellow, rest of antennae black; sides of clypeus at base, fairly wide anterior orbits from clypeus to lateral ocelli, a linear spot on posterior orbits just below temples, most of mandibles and all mentum, reddish; pronotum deep red; wings light yellow; teeth on posterior tibiae very small; a small species about 14.5 mm long. Ecuador .... *caesius* n. sp.

Specificity and Speciation in the Genus Cyrtosomum (Nematoda: Atractidae)[1]

JEROME J. GAMBINO and DONALD HEYNEMAN
Universtiy of California, Los Angeles

Four species are known in the atractid genus *Cyrtosomum* Gedoelst, 1919: *C. scelopori* Gedoelst, 1919; *C. penneri* Gambino, 1957; *C. readi* Gambino, 1958; and *C. heynemani* Gambino, 1958. Members of this genus of pinworms are found exclusively in the lizard family Iguanidae. They are apparently further restricted within that family to the North and Central American forms, judging from collecting records available (Pereira, 1935; Karve, 1938; Lent and Freitas, 1948).

Of the 765 specimens of iguanids examined for *Cyrtosomum spp.*, approximately 17 percent or 132, were infected. These infections were distributed as follows: *C. penneri* in 48 lizards (Table I), *C. heynemani* in 36 (Tables II and V), *C. readi* in 25 (Tables III and V), *C. scelopori* in 18 (Table IV). Dual infections of *C. heynemani* and *C. readi* (Table V) were found in 5 host specimens. All but one of the North and Central American genera of iguanids commonly recognized were represented, a total of 46 species and subspecies having been examined.

Among these hosts, *C. penneri* was found in 7 species, *C. heynemani* and *C. readi* in 5, and *C. scelopori* in 6. A single species was found with the dual infection. Table VI lists the 17 species which were found to be uninfected.

With the few exceptions shown in Table V, each species of parasite is specific for several closely related host species. The restriction of each of these nematodes to groups which are closely related taxonomically attests to the high degree of host-parasite specificity exhibited by the genus *Cyrtosomum*. The low incidence of dual and cross infections, despite considerable distributional and ecological overlap of the hosts, indicates a specificity that appears to be physiological rather than ecological. This is best illustrated by the material collected in the southern deserts and coastal mountains of California. Examination of over 300 lizards from this limited geographic region revealed neither dual nor cross infections, yet three of the four species of *Cyrtosomum* appear to have foci of infection in this area.

Taxonomic Considerations

The genus *Cyrtosomum* was divided into four distinct species based on evidence derived from adult morphology, variability, host specificity,

---

[1] These studies were aided by a contract between the Office of Naval Research, Department of the Navy, and the University of California, Los Angeles, NR 103-446.

and parasite distribution (Gambino, 1957a, 1957b, 1957c, 1958). This complex of ecological, physiological, and morphological criteria proved to be the most useful indicator of species separation. The most reliable morphological characters were those employing spicule ratios, which showed the least variability and the greatest concordance with other criteria. Characters employed were spicule ratio (Fig. 1); the ratio of the spicule ratio to body length (Fig. 2); and the ratio of the right spicule to body length compared with the ratio of the left spicule to body length (Fig. 3). Less reliable was the ratio of esophagus length to body length (Figs. 4 and 5), as both the esophagus and body length are subject to change due to contraction upon fixation. Since spicule length remains constant at fixation, ratios involving this structure were found to be more reliable than were total body measurements.

Lip papillae patterns and the number of male caudal papillae

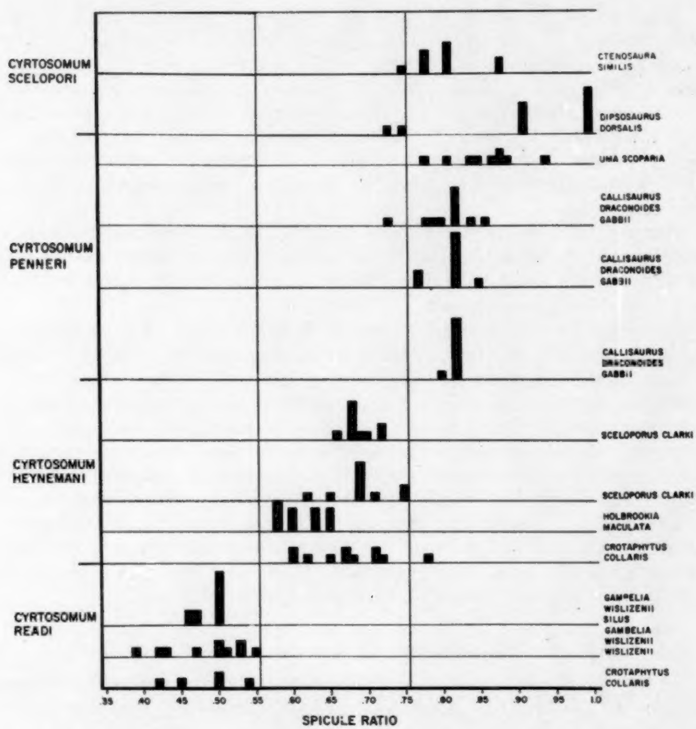


Fig. 1.—Histogram showing the use of the ratio between right and left spicule length as a morphological criterion of speciation in *Cyrtosomum*. Each square represents one specimen.

have been used in previous works in this and related genera and serve to separate *C. scelopori* from the other species in the genus. The latter character, however, is somewhat variable (Fig. 6) and should only be used in conjunction with other criteria.

Biological characters — life cycle, host specificity, and host distribution — gave the additional evidence which warranted division of this genus into four distinct species.

TABLE I.—Incidence and distribution of *Cyrtosomum penneri*

Host	Locality	No. Hosts Examined	No. Infected
Callisaurus draconoides carmenensis Dickerson	San Fransisquito Bay, Baja Calif., Mexico	2	2
C. d. gabbii Cope	Los Angeles Co., Calif.	6	0
	Riverside Co., Calif.	6	2
	San Bernardino Co., Calif.	13	3
	San Diego Co., Calif.	1	1
	Baja Calif., Mexico	34	13
	Sonora, Mexico	1	1
C. d. splendidus Dickerson	Angel de la Guarde Isl., Baja Calif., Mexico	7	5
Petrosaurus sp.	Baja Calif., Mexico	1	1
Sceloporus graciosus vandenburgianus Cope	San Bernardino Co., Calif.	18	2
S. magister rufidorsum Yarrow	Baja Calif., Mexico	1	1
S. occidentalis biseriatus Hallowell	Los Angeles Co., Calif.	74	7
	San Bernardino Co., Calif.	5	0
	San Luis Obispo Co., Calif.	2	0
Uma scoparia Cope	Riverside Co., Calif.	2	2
	San Bernardino Co., Calif.	8	7
Uta stansburiana Baird and Girard	Kern Co., Calif.	1	0
	Los Angeles Co., Calif.	46	1
	San Bernardino Co., Calif.	6	0
	Baja Calif., Mexico	1	0
	Unknown locality	3	0
Totals		238	48

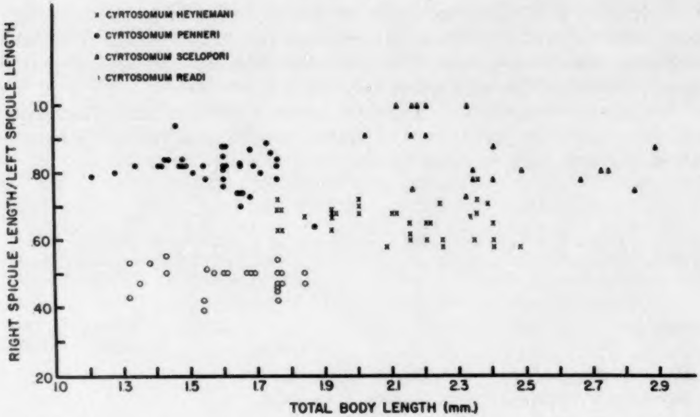


Fig. 2.—Spicule ratio plotted against total body length in *Cyrtosomum* spp.

Zoogeography of Cyrtosomum

C. scelopori has a wider host range and geographic distribution than any of the other species. This form infects *Ctenosaura similis, C. acanthura,*[2] *C. hemilopha, Enyaliosaurus quinquecarinatus,* and *Basiliscus vittatus* throughout the geographic ranges of all of these species, extending from Panama to the southern border of the United States (Fig. 7). In the United States the infection occurs in *Dipsosaurus dorsalis* and *Sauromalus obesus.* The rather limited ranges of these hosts indicate that a disjunct population of *C. scelopori* probably occurs in the United States. The ranges of *D. dorsalis* and *S. obesus* overlap the range of the most northern *Ctenosaura, C. hemophila,* only in Baja California, and there the *C. hemophila* population is an isolated one. *Sceloporus undulatus* is the type host of *Cyrtosomum scelopori,* but it appears that *Cyrtosomum* is only an incidental parasite in this host. Examination of 63 lizards from a wide geographic range revealed only two *Cyrtosomum* infections and these were *C. readi* and *C. heynemani,* not *C. scelopori.*

C. penneri was found in high incidence in three species of hosts: *Callisaurus draconoides, Uma scoparia,* and *Sceloporus occidentalis.* Although infections also occurred in *Sceloporus graciosus, S. magister,* and *Petrosaurus spp.,* too few of these animals were examined to draw conclusions regarding their suitability as hosts of *Cyrtosomum.* The single infection found upon examination of 57 specimens of *Uta stansburiana* indicates that this was an incidental infection. The geographic range of *C. penneri* is an extremely narrow one, extending from the

[2] Reported by Bravo-Hollis, 1942.

deserts and coastal ranges of southern California to Baja California.

Of the two remaining species, *C. readi* has a wider host distribution and a more varied geographic range than has *C. heynemani*. *C. readi* parasitizes *Phrynosoma asio,* a form with a range as far south as the southern states of Mexico, and infects *P. platyrhinos, P. m'calli* and *P. solare,* the horned lizards with ranges extending throughout the southwestern United States. *C. readi* also occurs in *Gambelia wislizenii* at the western extreme of its range.

The ranges of *C. readi* and of *C. heynemani* overlap in Arizona and New Mexico. The predominant form in these two states, however, is *C. heynemani*. *C. heynemani* occurs in *Holbrookia maculata, Sce-*

TABLE II.—Incidence and distribution of *Cyrtosomum heynemani*

Host	Locality	No. Hosts Examined	No. Infected
Holbrookia maculata Girard	Apache Co., Ariz.	1	0
	Cochise Co., Ariz.	2	1
	Navajo Co., Ariz.	4	3
	Pima Co., Ariz.	2	0
	Santa Cruz Co., Ariz.	8	7
	El Paso Co., Colo.	1	1
	Guadalupe Co., Mex.	2	0
	Otero Co., N. Mex.	3	1
	Socorro Co., N. Mex.	11	9
	Torrance Co., N. Mex.	1	1
	Tom Green Co., Texas	4	0
	Sonora, Mexico	4	0
	Chihuahua, Mexico	1	0
	Unknown locality	4	0
H. texana (Troschel)	Yuma Co., Ariz.	3	0
	Otero Co., N. Mex.	3	0
	Socorro Co., N. Mex.	28	2
	Tom Green Co., Texas	5	0
Sceloporus clarki Baird and Girard	Greenbee Co., Ariz.	1	1
	Santa Cruz Co., Ariz.	1	0
	Sierra Co., N. Mex.	2	0
	Sonora, Mexico	2	0
	Unknown locality	5	5
S. poinsetti Baird and Girard	Catron Co., N. Mex.	8	0
	Eddy Co., N. Mex.	5	1
	Socorro Co., N. Mex.	2	0
	Chihuahua, Mexico	10	0
S. woodi Stejneger	Broward Co., Florida	1	0
	Highland Co., Florida	6	1
Totals		132	33

loporus clarki, and *Crotaphytus collaris. Holbrookia texana, Sceloporus poinsettii,* and *Sceloporus undulatus* do not appear to be optimal hosts for *C. heynemani,* in view of the low incidence with this form.

Crotaphytus collaris affords a special case in which no barrier to either *C. readi* or *C. heynemani* appears to exist. An explanation for the source of the dual infections might be found in the lizard-eating habit of *C. collaris,* which may, therefore, represent a new host to which these parasites have secondarily become adapted. *C. collaris* occupies a wide geographic range which overlaps that of both parasites *C. readi* in California and *C. heynemani* in New Mexico. In California, a single infection of *C. readi* was reported. In New Mexico, one infection of *C. heynemani* and five dual infections involving these two species were examined, as previously noted.

Few examinations were made of Iguanidae from the eastern parts of the United States. No conclusions therefore can be drawn from the single infection of *C. heynemani* in *Sceloporus woodi* from Florida. Whether or not this represents a disjunct population of *Cyrtosomum* can be learned only from a study of the iguanids which have ranges extending across the southern and southeastern states.

PHYLOGENY OF CYRTOSOMUM

Three criteria considered indicative of increased specialization in *Cyrtosomum* include: reduction in the number of lip papillae, reduction in the number of caudal papillae, and reduction in the number

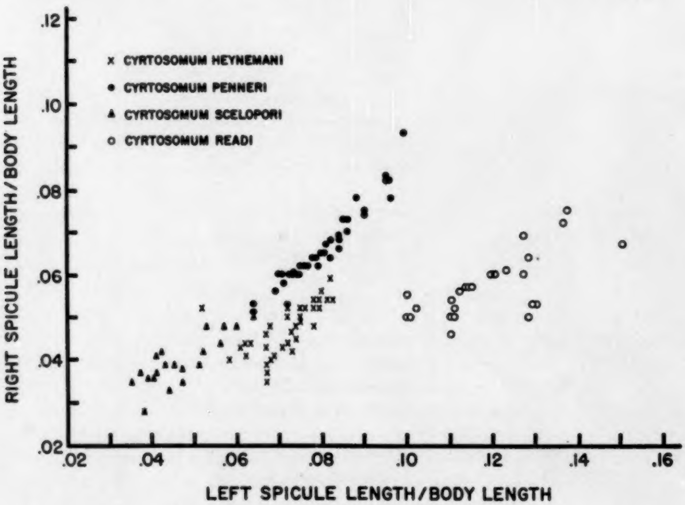


Fig. 3.—Right spicule ratio plotted against left spicule ratio in *Cyrtosomum* spp.

of host species. These criteria were used in this manner by Hetherington 1923; Thapar, 1925; Schuurmans Stekhoven, 1936; Chitwood and Chitwood, 1937; Filipjev and Stekhoven, 1941; Cameron, 1952, 1956; and Chabaud, 1954. According to these authors the reduction of sensory papillae in nematodes occurs concomitantly with increased specialization. Their view is based largely upon the nerves innervating these papillae, which persist despite the loss of the papillae themselves in the course of evolution.

Another indication that the loss of papillae is correlated with in-

TABLE III.—Incidence and distribution of *Cyrtosomum readi*

Host	Locality	No. Hosts Examined	No. Infected
Gambelia wislizenii silus Stejneger	Kern Co., Calif.	10	7
	San Bernardino Co., Calif.	2	0
G. w. wislizenii Baird and Girard	Coconino Co., Ariz.	1	0
	Imperial Co., Calif.	1	1
	Los Angeles Co., Calif.	21	4
	Riverside Co., Calif.	1	0
	San Bernardino Co., Calif.	7	1
	San Diego Co., Calif.	2	0
	Clark Co., Nev.	15	0
	Lyon Co., Nev.	1	1
	Socorro Co., N. Mex.	8	0
	Baja Calif., Mexico	1	1
	Unknown locality	1	0
Phrynosoma asio Cope	Mexico	2	1
P. m'calli Hallowell	Imperial Co., Calif.	1	0
	Riverside Co., Calif.	5	1
	San Diego Co., Calif.	2	0
P. platyrhinos Girard	Inyo Co., Calif.	2	2
	Kern Co., Calif.	1	1
	San Diego Co., Calif.	2	0
	Clark Co., Nev.	1	0
	Washoe Co., Nev.	1	0
P. solare Gray	Maricopa Co., Ariz.	1	0
	Pima Co., Ariz.	2	2
	Yavapai Co., Ariz.	1	1
	Sonora, Mexico	1	0
Totals		93	23

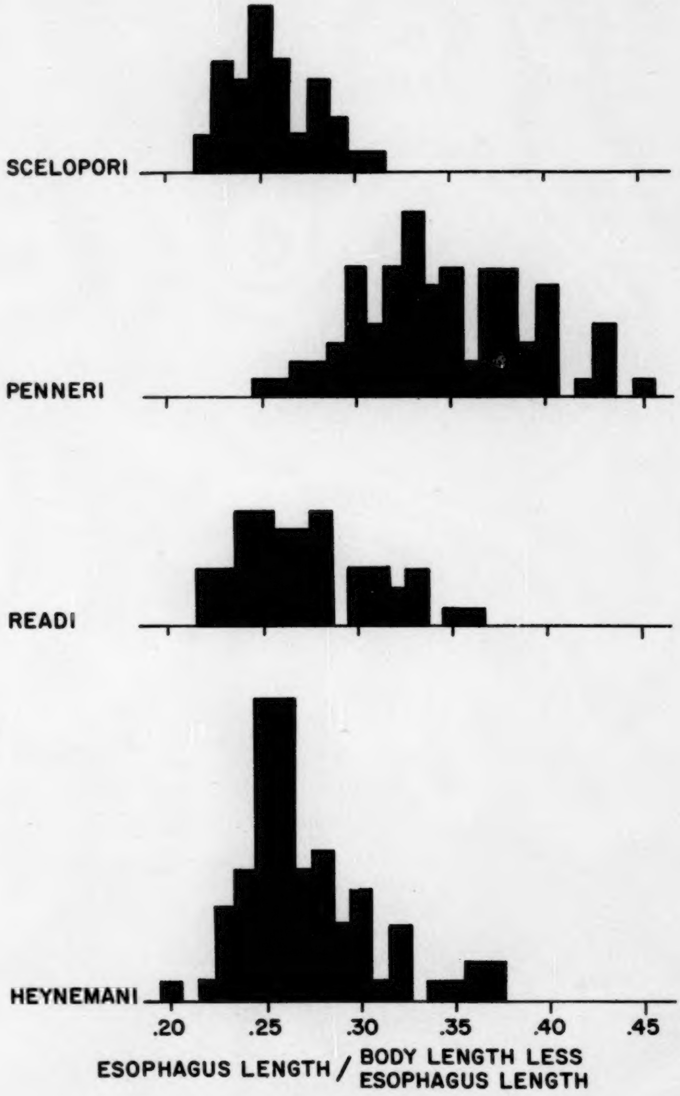


Fig. 4.—Histogram of esophagus-body ratio for each of the four species of *Cyrtosomum*.

creased specialization is found in a study of juvenile stages of the worms. Thapar (1925) reported the presence of certain caudal papillae in juvenile stages which are lacking in full mature adult stages of the same worm. Similar observations were made by one of the authors (Gambino) while studying the life cycle stages of *C. penneri*.

C. scelopori has 7 to 10 pairs of caudal papillae (Fig. 6, F), while *C. penneri, C. heynemani,* and *C. readi* all have either 6 or 7 pairs (Fig. 6). If this character were selected as a measure of divergence from a hypothetical ancestor, *C. scelopori,* which has the greatest number of caudal papillae, would be considered closest to the ancestral stem. The greater number of lip papillae in *C. scelopori* (see Plate II, Fig. F, Gambino, 1957a) can be considered additional evidence for this evolutionary position.

TABLE IV.—Incidence and distribution of *Cyrtosomum scelopori*

Host	Locality	No. Hosts Examined	No. Infected
Basiliscus vittatus Wiegmann	? Mexico	3	0
	Guerrero, Mexico	1	0
	Tierra Colorado, Mexico	3	0
	Vera Cruz, Mexico	2	1
	Zelaya, Nicaragua	1	0
	Panama	3	1
Ctenosaura hemilopha Cope	Sonora, Mexico	2	1
C. s. similis (Gray)	Managua, Nicaragua	2	1
Dipsosaurus d. dorsalis (Baird and Girard)	Mohave Co., Ariz.	4	0
	Inyo Co., Calif.	1	0
	Riverside Co., Calif.	15	4
	Clark Co., Nevada	7	2
	Unknown locality	3	1
Enyaliosaurus quinquecarinatus (Gray)	Oaxaca, Mexico	5	3
Sauromalus obesus (Baird)	Oatman Co., Ariz.	1	1
	Kern Co., Calif.	3	1
	Los Angeles Co., Calif.	1	1
	Riverside Co., Calif.	2	1
	San Bernardino Co., Calif.	4	0
	Clark Co., Nevada	1	0
Totals		64	18

Of the three remaining species, fully mature specimens of *C. penneri* have the smallest number of caudal papillae (usually 6 pairs) and on this basis represent the greatest divergence from the main stem, presumably being the most recently evolved (Fig. 6, B, C, E). Rarely, mature specimens of *C. penneri* possess 7 pairs of caudal papillae (Fig. 6, A). On the other hand, in both *C. readi* and *C. heynemani,* although 7 pairs is the usual number (Fig. 6, G, I), individuals with 6 pairs occasionally occur (Fig. 6, D. H). *C. heynemani,* more often than *C. readi,* possesses the reduced number and is therefore considered closer to *C. penneri. C. heynemani,* with a spicule ratio approaching that of *C. penneri* (Fig. 1), and on occasion having the same number of caudal papillae, is often difficult to distinguish from the latter species.

The following sequence, then, represents the divergence from a base form within the genus *Cyrtosomum,* measured in terms of male caudal papillae: *C. sceloporí, C. readi, C. heynemani,* and *C. penneri.*

Correlation with Host Evolution

C. penneri and *C. heynemani* occur in the fence lizard genus *Sceloporus,* and in the sand lizards *Uma, Callisaurus,* and *Holbrookia,* forms which are among the most recent iguanids (Mittleman, 1942; Savage, 1958). This conclusion seems to be corroborated by the presence of *C. penneri,* considered on morphological grounds to be the most specialized and recently evolved *Cyrtosomum,* in the genera *Uma* and *Callisaurus,* considered by the above authors as the most recent iguanids.

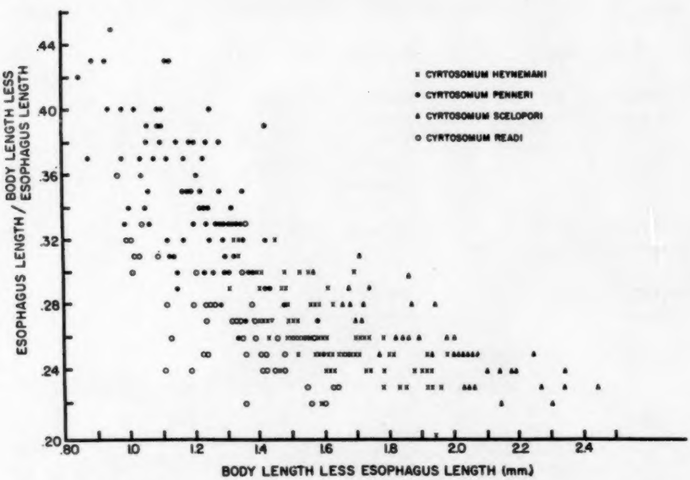


Fig. 5.—Esophagus-body ratio plotted against body length less esophagus length in *Cyrtosomum* spp.

C. readi, which appears to be an early branch of the *C. scelopori* line, is found in the genera *Gambelia, Crotaphytus,* and *Phrynosoma.* The first two genera have been synonymized by some students of the Iguanidae and are considered to have diverged from the main iguanid line extremely early in their evolutionary history. *Phrynosoma* also apparently diverged early from the main line of the Iguanidae, although its exact relationship within the family is somewhat obscure. Evidence of a relationship among these iguanid genera is suggested by their common pinworm parasite.

It appears significant that *C. scelopori,* which occupies the largest number of hosts and covers the widest geographic range, also possesses morphological characters generally considered to be primitive. Furthermore, its hosts are considered by other workers (Mittleman, 1942; Savage, 1958) to be the most primitive iguanids. Both of these lines of evidence therefore suggest that *C. scelopori* most nearly represents the

TABLE V.—Incidence and distribution of dual-infections (*Cyrtosomum readi* and *C. heynemani*) and cross-infections

Host	Locality	Number Hosts Examined	Number Infections	Parasite Species
Crotaphytus	Navajo Co., Ariz.	1	0	....
collaris Say	San Bernardino Co.			
	Calif.	2	1	*C. readi*
	Guadalupe Co., N. Mex.	1	0	....
	Lincoln Co., N. Mex.	2	1	dual
	Otero Co., N. Mex.	1	1	*C. heynemani*
	San Miguel Co., N. Mex.	1	1	dual
	Sierra Co., N. Mex.	1	0	....
	Socorro Co., N. Mex.	8	3	dual
	Torrance Co., N. Mex.	1	0	....
	Eastland Co., Texas	3	0	....
	Terrell Co., Texas	1	1	*C. heynemani*
Sceloporus	Fulton Co., Georgia	1	0	....
undulatus	Bernallilio Co., N. Mex.	1	0	....
(Daudin)	Catrone Co., N. Mex.	5	0	....
	Eddy Co., N. Mex.	2	1	*C. readi*
	Otero Co., N. Mex.	1	0	....
	San Miguel Co., N. Mex.	5	0	....
	Socorro Co., N. Mex.	18	1	*C. heynemani*
	Torrance Co., N. Mex.	14	0	....
	Union Co., N. Mex.	1	0	....
	Washington Co., Utah	10	0	....
	Norfolk Co., Virginia	4	0	....
	Totals	84	10	

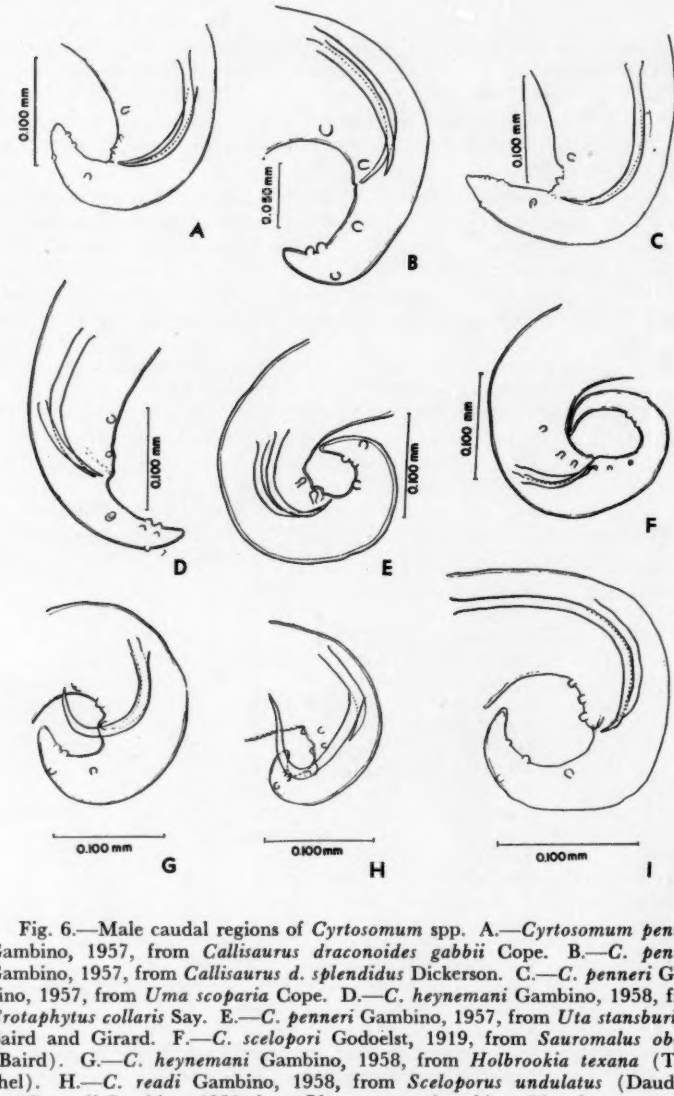


Fig. 6.—Male caudal regions of *Cyrtosomum* spp. A.—*Cyrtosomum penneri* Gambino, 1957, from *Callisaurus draconoides gabbii* Cope. B.—*C. penneri* Gambino, 1957, from *Callisaurus d. splendidus* Dickerson. C.—*C. penneri* Gambino, 1957, from *Uma scoparia* Cope. D.—*C. heynemani* Gambino, 1958, from *Crotaphytus collaris* Say. E.—*C. penneri* Gambino, 1957, from *Uta stansburiana* Baird and Girard. F.—*C. scelopori* Godoelst, 1919, from *Sauromalus obesus* (Baird). G.—*C. heynemani* Gambino, 1958, from *Holbrookia texana* (Troschel). H.—*C. readi* Gambino, 1958, from *Sceloporus undulatus* (Daudin). I.—*C. readi* Gambino, 1958, from *Phrynosoma platyrhinos* Girard.

ancestral type within the genus, and has therefore remained relatively unchanged during the course of evolution of the other members of the genus. In contrast, the other species, *C. readi, C. heynemani,* and *C. penneri,* in that order, appear to represent more recent and specialized offshoots of the *C. scelopori* line.

In view of the lack of information on other characters which might show phylogenetic relationship, it appears unwise at this time to sug-

TABLE VI.—Forms examined and found negative for *Cyrtosomum* spp.

Host	Locality	No. Hosts Examined
Anolis carolinensis Voigt	from Biological Supply Co.	60
Callisaurus draconoides inusitatus Dickerson	Sonora, Mexico	9
Iguana iguana (Linnaeus)	from Biological Supply Co.	10
Phrynosoma cornutum (Harlan)	San Miguel Co., N. Mex.	1
	Socorro Co., N. Mex.	2
P. modestum Girard	Socorro Co., N. Mex.	5
	Brewster Co., Texas	1
Sceloporus magister magister Hallowell	Santa Cruz Co., Ariz.	1
	Kern Co., Calif.	1
	Los Angeles Co., Calif.	6
	San Bernardino Co., Calif.	1
	Socorro Co., N. Mex.	2
S. o. orcutti Stejneger	Riverside Co., Calif.	8
S. scalaris sleveni Smith	Chihuahua, Mexico	1
S. torquata Wiegmann	Amecameca, Mexico	9
	Durango, Mexico	1
S. v. variabilis Wiegmann	Oaxaca, Mexico	1
Streptosaurus mearnsi (Stejneger)	Riverside Co., Calif.	2
Urosaurus auricularis (Cope)	Socorro Isl. Revillagigedo Archipelago, Mexico	8
U. bicarinatus (Dumeril)	Tierra Colorado, Mexico	4
U. microscutatus (Van Denburgh)	San Diego Co., Calif.	4
	Baja Calif., Mexico	2
U. ornatus chiricahue (Mittleman)	Cochise Co., Ariz.	4
U. o. symmetricus (Baird)	Riverside Co., Calif.	1
	Clark Co., Nevada	2
Uta graciosus (Hallowell)	Baja Calif., Mexico	1
	Totals	154

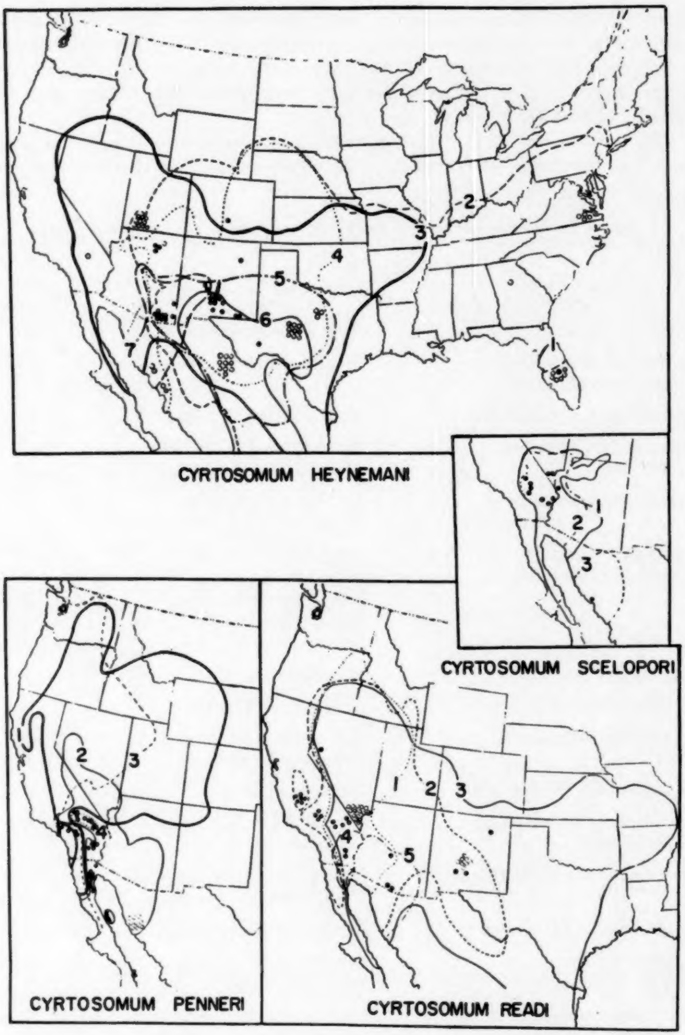


Fig. 7.—Geographic distribution of *Cyrtosomum* spp. and their hosts. The host ranges are numbered to correspond with the species listed below. Infected individuals are indicated by filled circles. Open circles represent uninfected individuals that mark the limits of the collecting range. *Cyrtosomum heynemani* Gambino, 1958: 1. *Sceloporus woodi;* 2. *Sceloporus undulatus;* 3. *Crotaphytus collaris;* 4. *Holbrookia maculata;* 5. *Holbrookia texana;* 6. *Sceloporus poinset-*

gest an exact phylogeny. It seems justifiable, however, to suggest a general sequence of speciation, utilizing those structures which have evolutionary significance according to most students of parasitic nematodes, especially when these criteria can be correlated with zoogeographic and ecological data.

In the evolution of specificity in the genus *Cyrtosomum,* a physical separation of the parasites in widely separated hosts appears to have allowed an accumulation of differences which seem to be physiological ones judging from the collecting data. Assuming this to be the case, the parasites would then become less capable of surviving in other hosts, even in closely related ones. Since the genus *Cyrtosomum* is confined to the Iguanidae, it may be hypothesized that at some time in the early history of both the Atractidae and the Iguanidae, an ancestral iguanid was parasitized by a form similar to *C. scelopori.* A long association between the parasite and its host would presumably have led to an adaptive physiological adjustment between the two, leading to a degree of dependence of the parasite upon its particular host. As some of the host species separated geographically and became morphologically distinct, the parasites accompanying them ultimately did the same. The morphological changes in these parasites appeared as minor cuticular modifications — nematodes being an unusually conservative group in terms of gross morphological changes in evolution. Parallel evolution of the parasite and host presumably maintained the specificity. Some of the host species, on the other hand, appear by their parasites to have diverged less markedly, or perhaps the intestinal environment available to their pinworm parasites remained more uniform. The ancestral species of *Cyrtosomum* was therefore able to parasitize these hosts without undergoing extreme modification or developing a high degree of physiological specificity. The more extreme cases of nematode specificity appear to imply a parallel evolution of host and parasite, marked by morphological divergence and increased dependence of the parasite on its host species. It does not, however, indicate the duration of this association since the adaptive modifications of the worms would vary with the rate of evolution of their hosts. Furthermore, the physiological aspects of this relationship can only be assumed (as in this example) except where laboratory cross-infectivity experiments are available. A host-parasite specificity which is ecological could be a chance occurrence of very recent origin. One which is physiological *might* be a product of long association and thus indicate a phylogenetic relationship. Speculations on the parallel evolution of host and parasite must always assume that the latter condition exists. This should be recognized as an assumption and should

---

tii; 7. Sceloporus clarki. Cyrtosomum scelopori Gedoelst, 1919 (full range of hosts not illustrated): 1. *Sauromalus obesus;* 2. *Dipsosaurus dorsalis;* 3. *Ctenosaura hemilopha. Cyrtosomum penneri* Gambino, 1957: 1. *Sceloporus graciosus;* 2. *Callisaurus draconoides;* 3. *Sceloporus occidentalis;* 4. *Uma scoparia. Cyrtosomum readi* Gambino, 1958: 1. *Phrynosoma platyrhinos;* 2. *Gambelia wislizenii;* 3. *Crotaphytus collaris;* 4. *Phrynosoma m'calli;* 5. *Phrynosoma solare.*

be a primary consideration to prevent any undue conclusions on host relationships based upon parasite specificity. Failure to recognize this assumption in many works has rendered their conclusions highly questionable and even raised doubts as to the validity of the procedure as a proper tool for the study of phylogeny. These limitations to phylogenetic speculations from host-parasite relations were emphasized by Mayr, Baer, Dubois, Chabaud, and others in their discussions reported in the "First Symposium on host specificity among parasites of Vertebrates" (Baer, 1957). Chabaud (*loc. cit.*: 317) divided specificity into two general types, *recent* and *ancient*. In the former type he placed three degrees, showing increasing specificity: *ecological, physiological,* and *neogenic*. These categories of recent specificity he considered to be independent of the systematic position of the host and hence of no value in evolutionary speculation. The other type of specificity, ancient or primitive specificity, he considered to be of phylogenetic significance. His choice of terms is unfortunate as physiological adaptation could accompany both types of specificity, and would be expected to occur in cases of phylogenetic importance. However, the necessity of distinguishing between accidental or ecological specificity and specificity which is of phylogenetic value is clear. One must look for host relationships from parasite data only in those instances where reasonably good evidence of a physiological genetically-determined dependence on a particular host exists, giving a good probability of parallel evolution. Experimental cross-infectivity tests must always be the ultimate arbiter used to clarify the question of ecological *vs.* phylogenetic specificity.

Several valuable studies have been made which do appear to have application to host phylogeny (Baer, 1947; Cameron, 1952; Clay, 1957; Hopkins, 1949; Rothschild and Clay, 1952). These deal chiefly with the most host specific groups of parasites, such as Mallophaga, Anoplura, certain cestodes, and restricted groups of Nematoda and Monogenea. It seems clear that good phylogenetic evidence from parasites is available, but that each case must be carefully analyzed for alternative explanations.

In the case of nematodes the problem is complicated by the difficulty of specific identification and the possibility of physiological specificity occurring with minimal morphological changes. Hence, it is necessary to depend upon relatively few morphological features, such as the lip or caudal papillary patterns. Nonetheless, these criteria seem to be reliable indices and have therefore been used in the present study.

The more specialized species of *Cyrtosomum* considered in this report are presumably the derived species, more recently evolved and found in more recent host species as well, whereas the least host specific and the least specialized form, found in the most primitive hosts, is considered the oldest parasite species. This contravenes the common assumption that degree of specialization is an index of evolutionary age of a species, and therefore a more specialized, host-specific para-

site would presumably indicate a greater degree of adaptation and a greater age of parasitism. It appears that in this example the primitive host, remaining essentially unchanged, offered a relatively stable and constant environment for its pinworm parasites. No new selective physiological factors acted upon them, and, as with the classic instance of the ancient branchiopod *Lingula,* the same species remained unchanged so long as the environment and the forces of natural selection were unchanged. In the case of parasites which found themselves in more rapidly evolving hosts, different selective pressures were involved. This changing environment would presumably result in the selecting out of new, better adapted variants, specifically adapted to the new host species. Hence, the more specialized and specific parasite species would be the most recently evolved.

SUMMARY

A morphological and distributional analysis was made of the four species of pinworms in the nematode genus *Cyrtosomum.* These are all parasitic in the lizard family Iguanidae and show a marked degree of host specificity which serves as a guide to understanding the evolution in this genus of parasites. The species studied include *Cyrtosomum scelopori* Gedoelst, 1919; *C. penneri* Gambino, 1957; *C. readi* Gambino, 1958; and *C. heynemani* Gambino, 1958. Some 765 iguanid lizards, of 46 species and subspecies, were examined and 17 percent of the individuals were infected. Each parasite was found in 5 to 7 species of hosts and was not found in host species parasitized by other *Cyrtosomum* species except for a few instances of dual infections of *C. heynemani* and *C. readi* in one host species.

Utilizing the morphological criteria of various ratios of spicule to body measurements, the pattern of lip and caudal papillae, and the evidence from parasite distribution and host specificity, the following phylogenetic sequence is proposed: *C. scelopori,* as the oldest, least specialized, and least host specific; *C. readi, C. heynemani,* and *C. penneri,* as more recent successive stages of increased morphological modification and host specificity.

A discussion of the application of such data to the interpretation of host phylogeny is included.

Those species of *Cyrtosomum* which show the greatest morphological change and the maximum host specificity (*C. penneri* and *C. heynemani*) appear to have passed through a more vigorous period of selection in a more rapidly fluctuating environment; (*e.g.*: more rapidly evolving host species) than did the more primitive worms (*C. scelopori* and *C. readi*). These morphological and physiological changes are thought to have occurred despite the fact that the presumably specialized species have not been in their hosts for as long a time as have the worms from which they arose. The latter form, *C. scelopori,* remained in the less rapidly changing environment of its primitive hosts without developing as marked a host specificity or undergoing as apparent a morphological change as did the others.

REFERENCES

BAER, JEAN G. 1947. Les helminthes parasites des Vertébrés. Relations phylogéniques entre évolution et celle de leurs hôtes. *Ann. Sc. Franche-Comté,* **2**:99-113.

———1957. (ed.) *First Symposium on host specificity among parasites of Vertebrates.* Neuchatel. 324 pp.

BRAVO HOLLIS, M. 1942. Acerca de un nematodo parasito de la iguana (*Ctenosaura acanthura* (Shaw)). *An. Inst. Biol., Univ. Nac. México,* **13**: 533-537.

CAMERON, T. W. M. 1952. Parasitism, evolution and phylogeny. *Endeavour,* **11**:193-199.

———1956. *Parasites and Parasitism.* Wiley, New York. 332 pp.

CHABAUD, A. G. 1954. Sur le cycle évolutif des spirurides et de nématodes ayant une biologie comparable. Valeur systématique des caractères biologiques. *Ann. Parasitol.,* **29**:42-88, 206-249, 358-425.

CHITWOOD, B. G. AND M. B. CHITWOOD 1937. *An Introduction to Nematology. Sect. I, Anatomy.* Published by the authors, Baltimore. 213 pp.

CLAY, T. 1957. The Mallophaga of birds. In *First Symposium on host specificity among parasites of Vertebrates.* J. G. Baer (ed.). Neuchatel. pp. 120-156.

FILIPJEV, I. N. AND J. H. SCHUURMANS STEKHOVEN, JR. 1941. *A Manual of Agricultural Helminthology.* E. J. Brill, Leiden. 878 pp.

GAMBINO, J. J. 1957a. *Cyrtosomum penneri* n. sp. (Oxyuroidea; Atractidae). *J. Parasitol.,* **43**:76-80.

———1957b. Relationships of North American Iguanidae as suggested by an analysis of their pinworm parasites, *Cyrtosomum* spp. *Anat. Record,* **128**:553-554.

———1957c. A biological study of the nematode genus *Cyrtosomum,* pinworms of iguanid lizards of North America. Doctoral Dissertation, University of California, Los Angeles, California.

———1958. *Cyrtosomum readi* n. sp. and *Cyrtosomum heynemani* n. sp. (Oxyuroidea; Atractidae). *J. Parasitol.,* **44**:439-445.

HETHERINGTON, D. C. 1923. Comparative studies on certain features of nematodes and their significance. *Illinois Biol. Monogr.,* **8**:1-62.

HOPKINS, G. H. E. 1949. The host-associations of the lice of mammals. *Proc. Zool. Soc. London,* **119**:387-604.

KARVE, J. H. 1938. Some nematode parasites of lizards. *Livro Jub. Travassos,* pp. 251-258. Rio de Janeiro.

LENT, H. AND J. F. TEIXEIRA DE FREITAS 1948. Uma coleção de nematódeos, parasitos de vertebrados do museu de historia natural de Montevideo. *Mem. Inst. Oswaldo Cruz,* **46**:1-71.

MITTLEMAN, M. B. 1942. A summary of the iguanid genus *Urosaurus. Bull. Mus. Comp. Zool.,* **91**:103-181.

PEREIRA, C. 1935. Os Oxyurata parasitos de Lacertilia do nordeste Brasileiro. *Arch. Inst. Biol., São Paulo,* **6**:5-27.

ROTHSCHILD, M. AND CLAY. T. 1952. *Fleas, Flukes and Cuckoos, a Study of Bird Parasites.* Philosophical Library, New York. 304 pp.

SAVAGE, JAY M. 1958. The iguanid lizard genera *Urosaurus* and *Uta* with remarks on related groups. *Zoologica,* **43**(2 and 3):41-54.

SCHUURMANS STEKHOVEN, J. H., JR. 1936. Nematodes. *In* H. G. Bronn (ed.), *Klassen und Ordnungen des Tierreichs,* v. 4 Abt. 2, Buch **3**:65-364.

THAPAR, G. S. 1925. Studies on the oxyurid parasites of reptiles. *J. Helminth.,* **3**:83-150.

Host Relationships of Some Eastern Siphonaptera

ALLEN H. BENTON[1] and ROBERT H. CERWONKA[2]
State University of New York

Although the biology of a few species of fleas has been carefully studied because of their importance as vectors of human disease organisms, few detailed studies of host specificity have been made. Since 1952 the senior author and his students at New York State College for Teachers, Albany, in collaboration with the New York State Museum and Science Service, have made intensive collections of fleas in eastern New York. These joint collections have now reached a total in excess of 2000 specimens, parts of which have been previously noted in papers by Sturm (1953), Cummings (1954), Benton, (1955), Benton and Krug (1956), and Connor (1959). In addition to the data on geographical distribution, which will be the subject of another paper, these specimens have provided much-needed information on host-parasite relationships and have clarified several uncertainties as to the "true" or preferred host of certain flea species. These data, along with information from other published and unpublished sources, are sufficient to permit a detailed consideration of host relationships in most of the species involved.

The host relationships of fleas from a world viewpoint have been ably discussed by Hopkins (1958). To be useful to the student of flea-borne diseases, mammalian ecology, and other problems of host-parasite ecology, this work needs to be supplemented by full information on the host distribution of each species. Available information usually falls short of fulfilling the needs of the student of host relationships, and an awarness of the special problems of such studies may help future collectors to make greater contributions to knowledge.

The study of host relationships in fleas is complicated by the fact that these insects, unlike most ectoparasites, are not closely tied to life on the host. Their agility, their leaping ability, and their capacity to survive for long periods of time without food make it possible for them to leave and return to the host many times during a lifetime. Thus accidental associations may occur when fleas leap upon a passing animal other than the usual host. In the Northeast, a single woodland burrow may be occupied, in the course of a few days, by eight to ten different species of rodents and insectivores, so that fleas lying in wait along the burrow or in nest cavities may often reach the wrong host quite by accident.

Accidental associations are also the result of predation. Most of our predators are apparently without specific fleas, although they often carry fleas which belong on their prey animals. Records of fleas from

---

[1] College for Teachers, Albany.
[2] Teachers College, Potsdam.

predators are therefore generally useless in evaluating host relationship of the parasites.

Another factor which has led to much confusion as to host relationships is the relative abundance of various hosts. For example, *Hystrichopsylla tahavuana,* an apparently rare flea in the northeast, is most often taken from the short-tailed shrew, *Blarina brevicauda.* But this is largely because *Blarina* is taken in such tremendous numbers by mammal collectors. On a proportional basis, this flea is much more common on moles, *Parascalops breweri* and *Condylura cristata,* which are probably the preferred hosts.

There is some evidence, also, that ecological requirements other than the presence of a particular host may be significant in flea distribution. Definite patterns of altitudinal distribution in certain species (e.g. *Orchopeas caedens durus* in New York) are most easily explained on such a basis. The true host, the red squirrel (*Tamiasciurus hudsonicus*) occurs throughout the state, but the flea has thus far been taken only in the Adirondack Mountains.

In spite of these pitfalls, it seems worthwhile at this time to summarize the data on host relationships which can be gained from study of the above mentioned collections. In some cases data from other published and unpublished reports have been used to supplement our data.

This study has been supported by a grant from the Research Foundation of State University of New York. The collections on which

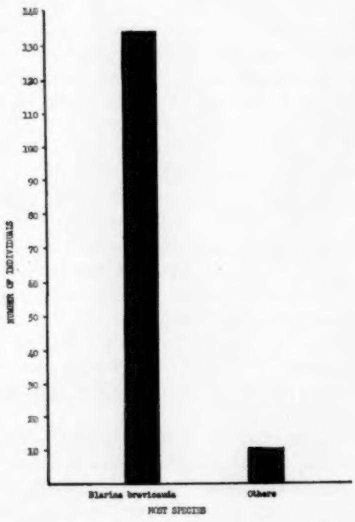


Fig. 1.—Host distribution of 142 specimens of *Doratopsylla blarinae.*

this paper is largely based were made by Paul Connor, Edward Cummings, Arnold Dansky, R. F. Krug, Donald Miller, Daniel Smiley, Robert Sturm and the authors. We are grateful especially to G. H. E. Hopkins, of the British Museum (Natural History) for advice and suggestions from his wide and intimate knowledge of fleas; for critical reading of the manuscript; and for suggesting the classification of host relationships which follows.

A Classification of Host Relationships

Since the true biological basis of flea-host relationships is not always apparent, it will be convenient to group the species according to the degree of host specificity which they exhibit. We may place the species in one of five groups, as follows:

Class 1: Species which are obligate parasites of a single host species, although they may occur accidentally on other animals. Such species may often be detected by the fact that their range is coincident with that of the host (Fig. 1).

Class 2: Species which are able to exist as parasites of two or more species of closely related hosts, though showing a definite host preference. Such species often occur on one host in a given area, and upon another host outside the range of the first (Fig. 2).

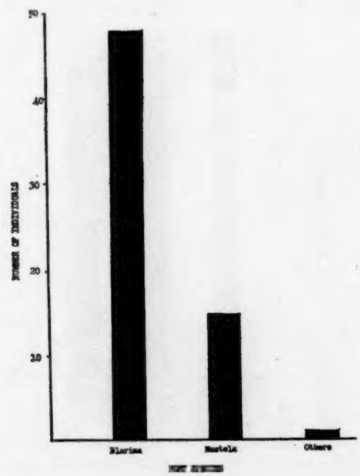


Fig. 2.—Host distribution of 53 specimens of *Nearctopsylla genalis laurentina.*

Class 3: Species which are able to exist as parasites of two or more species and within that group of hosts show little or no host preference. Hosts of the same genus or of closely related genera are often infested by such fleas with no apparent preference being shown in collection data. (Fig. 3).

Class 4: Species which feed on a variety of hosts and are not dependent upon any one species or group, but which nevertheless show a definite preference for a particular species or group (Fig. 4).

Class 5: Species which show no apparent host preference, occurring on a wide variety of unrelated host animals in approximately equal numbers. This does not exclude the possibility that the flea may be limited in host distribution by other factors, such as size of host, type of nest of host, etc. (Fig. 5).

Eventual proof of host associations and relationships must rest upon experimental data, rather than upon deductions from collections. However, the large numbers of specimens at our disposal permit a more accurate appraisal of host relationships than has heretofore been possible.

ACCOUNTS OF SPECIES

The classification which follows includes all the species of fleas

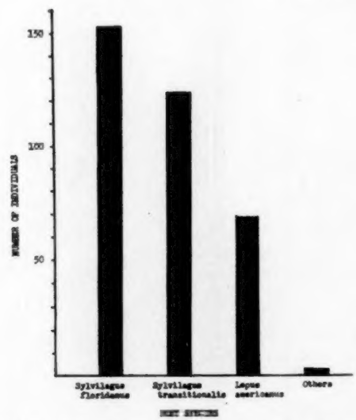


Fig. 3.—Host distribution of 349 specimens of *Cediopsylla simplex*. Greatest number was taken from *Sylvilagus floridanus* because that host was taken in greatest numbers. Number of fleas per host is about equal in all three species of rabbit hosts.

which we have collected in eastern New York. Those species for which the data are few or inconclusive are indicated by an asterisk. Our arrangement of families follows that of Hopkins and Rothschild (1953). The number in parentheses following the host relationship class designation indicates the number of individuals we have collected.

FAMILY PULICIDAE

Cediopsylla simplex (Baker).—This flea is confined to rabbits, although it often occurs upon their predators. In eastern New York it occurs without apparent preference upon all three native species of Leporidae, *Lepus americanus, Sylvilagus floridanus* and *S. transitionalis.* Class 3. (349).

Ctenocephalides canis (Curtis).—Although our single record of the dog flea is insufficient to permit a guess as to host relationships, abundant records from other places indicate that the domesticated dog, *Canis familiaris,* is the preferred host. It is also found on foxes, coyotes, and occasionally on other hosts. Our single record is from the red fox, *Vulpes fulva.* Class 2. (1).

FAMILY HYSTRICHOPSYLLIDAE

**Atyphloceras bishopi* Jordan.—Although widely distributed, this species seems to be difficult to secure, and few records are available. Our records are mostly from *Microtus pennsylvanicus,* but Fuller (1943) secured 27 specimens from *Clethrionomys gapperi.* It is thus quite certainly a parasite of Microtinae, although it is not possible to tell which, if either, of these species is the more frequent host. Class 2 or 3. (20).

**Hystrichopsylla tahavuana* Jordan.—This large flea has been taken in approximately equal numbers in eastern New York on *Parascalops breweri, Condylura cristata* and *Blarina brevicauda.* Because of the large numbers of *Blarina* which are taken, and the small numbers of the moles which fall to the trapper, it seems likely that the moles are preferred hosts. Class 3. (14).

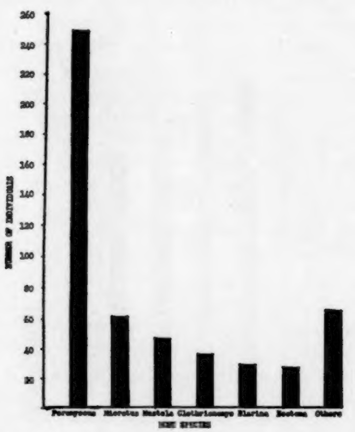


Fig. 4.—Host distribution of 509 specimens of *Epitedia wenmanni.*

**Stenoponia americana* (Baker).—About half of the specimens of this species which have been reported in the literature were taken from deermice (*Peromyscus*), with the rest coming from a wide variety of small mammals. This giant flea is not commonly taken, and further collecting is essential before its host relationships will be clear. Class 4. (27).

**Catallagia borealis* Ewing [= *C. onaga* Jordan].—The only sizable collection of this species was reported by Fuller (1943) from the red-backed mouse, *Clethrionomys gapperi*. It has also been collected several times from *Blarina brevicauda*. Its rarity in collections makes it impossible at present to evaluate its host relationships. Class unknown. (3).

Epidetia wenmanni wenmanni (Rothschild) and *E. w. testor* (Rothschild). —Throughout its wide range, this species is most commonly associated with *Peromyscus*, but it occurs so often on a variety of small mammals that its connection to this genus must not be a very close one (Benton, 1955). Class 4. (41).

**Epitedia faceta* (Rothschild).—Although the red squirrel, *Tamiasciurus hudsonicus*, is the type host of this flea, our records indicate that the flying squirrel, *Glaucomys volans*, is the usual host. Our specimens have been taken in the colder months, indicating that extensive collecting in winter might supply enough specimens to clarify this matter. Class 1 or 2. (24).

Tamiophila grandis (Rothschild).—This large flea is almost never recorded from any host other than the chipmunk, *Tamias striatus*. Relatively few specimens have been taken but its host relationship is clearly apparent. (Class 1. (17).

Ctenophthalmus pseudagyrtes pseudagyrtes Baker.—This is at the same time one of the most common fleas and the least host-specific flea occurring in our area. Fleas found on odd hosts such as skunks, porcupines, or other hosts having no flea fauna of their own are most likely to be of this species. On these hosts it sometimes occurs in considerable numbers. Pine mice, lemming mice, and jumping mice are among the species which have no specific fleas in this area but which often harbor *Ctenophthalmus* in fair numbers. Class 5. (249).

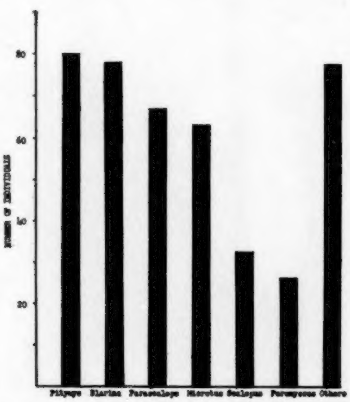


Fig. 5.—Host distribution of 422 specimens of *Ctenophthalmus pseudagyrtes*.

Doratopsylla blarinae C. Fox.—Krug and Benton (1953) collected 46 fleas of this species without recording one from any host other than the short-tailed shrew. This is an indication of its close affinity for this shrew. Occasionally it occurs on other mammals which are ecologically associated with its true host, but even such occurrences are rare. Class 1. (142).

**Corrodopsylla curvata curvata* (Rothschild).—This species is reported by Holland (1949) to be most closely associated with the genus *Sorex,* although it has been reported frequently from *Blarina.* At the present time insufficient numbers are available to permit a conclusion as to its preferences within the shrew family. Class 3. (2).

**Conorhinopsylla stanfordi* Stewart.—The red squirrel, *Tamiasciurus hudsonicus,* is the type host of this seemingly rare flea, and one of our specimens comes from the gray squirrel, *Sciurus carolinensis.* Failure to secure it from large collections of the red squirrel (*e.g.,* Layne, 1954), has led to doubt as to its association with this host. Our collections have been almost exclusively from the flying squirrel, *Glaucomys volans,* and it seems likely that further collections will show this to be the preferred host. Class 2. (20).

Nearctopsylla genalis laurentina Jordan and Rothschild.—Although we have a rather large series of this flea, its host relationships are not entirely clear. The short-tailed shrew is the most frequent host, and we have a fairly large series from weasels, probably the result of predation. It occurs on other shrews, and less commonly on moles, indicating that the class 2 designation is probably the correct one. Class 1 or 2. (53).

Oropsylla arctomys (Baker).—Within our area, this flea occurs only on the woodchuck, *Marmota monax,* but in other sections it occurs on other marmots. Occasional records from rabbits and predators are no doubt accidental. Class 2. (22).

Opisodasys pseudarctomys (Baker). — Although most often taken from *Glaucomys sabrinus,* the northern flying squirrel, this flea is also known to occur in nests and on individuals of *G. volans.* It has been taken in sufficient numbers from both these species to indicate that it can survive as a host of either, though evidently occurring most abundantly on the former. Class 2. (67).

Orchopeas caedens durus (Jordan).—*Orchopeas caedens* is a specific parasite of the red squirrel, *Tamiasciurus hudsonicus.* In the east, however, it does not occur throughout the range of this squirrel, thus presenting a very interesting problem in the causation of flea distribution. It occurs in the Adirondacks, and possibly in the Catskill Mountains as well, although it has not yet been collected there. To the south, and apparently wherever the range of the red squirrel overlaps that of the gray squirrel, *Sciurus carolinensis,* this flea is replaced by *O. howardii.* We have not thus far collected both species of flea from the same squirrel or from the same locality. Class 1. (39).

Orchopeas leucopus (Baker).—This abundant flea occurs with apparent indifference on our two deermice, *Peromyscus leucopus* and *P. maniculatus.* Other occurrences on ecological associates of these mammals are sufficiently uncommon to be considered accidental. Class 3. (456).

Orchopeas sexdentatus pennsylvanicus (Jordan).—A true parasite of the woodrat, *Neotoma magister,* this species occurs wherever this host occurs. It has not been found in regular association with any other species. Class 1. (17).

Orchopeas howardii howardii (Baker).—This flea has a close affiliation with the gray squirrel, *Sciurus carolinensis,* and apparently does not occur to the north of the range of this host (Holland, 1949). Although this evidence would

appear to place it as a Class 1 flea, its occurrence in large numbers on *Glaucomys* and *Tamiasciurus* indicate an ability to survive as a parasite of these squirrels as well. In the south it occurs in large numbers on the fox squirrel, *Sciurus niger*. Class 2. (230).

**Ceratophyllus gallinae* Schrank.—The chicken flea will bite rats and man, as well as various species of domestic poultry, but seems unable to establish itself on any mammal. Our collection of this species, from *Rattus norvegicus*, sheds no light on its true affiliations. Class 2. (1).

Megabothris acerbus (Jordan).—The eastern chipmunk, *Tamias striatus*, is the host of this highly specific flea, which is rarely taken on any other animal. Class 1. (43).

Megabothris asio asio (Baker). — This appears to be a nest flea, and is seldom taken from trapped animals, so that its host distribution is difficult to evaluate. In our area, however, it seems to be a parasite of the meadow vole, *Microtus pennsylvanicus*, from whose nests most of our specimens were taken. Class 1. (27).

**Megabothris quirini* (Rothschild).—Evidence indicates that this species is associated with the red-backed mouse, *Clethrionomys gapperi*, but it has been taken so rarely in our area that its host relationship is not definite. Its apparent rarity may indicate that it, like *M. asio*, is primarily a nest flea. Collectors should examine nests of the red-backed mouse to secure data on this point. Class 1. (11).

Monopsyllus vison (Baker).—This species is a parasite of the red squirrel, and is not known from any location where red squirrels do not occur. Where both red and gray squirrels occur, however, it may be found in some numbers on the gray squirrel (Wells, 1957). Class 1. (17).

Nosopsyllus fasciatus (Bosc).—Because this flea is a parasite of the Old World mice and rats, it has been collected in tremendous numbers in Public Health Surveys. These surveys show it to be found primarily on the Norway rat, *Rattus norvegicus*, the black rat, *Rattus rattus*, and the house mouse, *Mus musculus*, with some apparent preference for the Norway rat. Class 2. (12).

FAMILY LEPTOPSYLLIDAE

Peromyscopsylla catatina (Jordan).—This flea has been taken from several hosts, but evidence from its local distribution in eastern New York indicates that it is a true parasite of the red-backed vole, *Clethrionomys gapperi*. Most of our specimens come from this host, and we have never taken this flea in any area where red-backed voles do not occur. Class 1. (34).

Peromyscopsylla h. hesperomys (Baker).—In our area, this species occurs without apparent preference on *Peromyscus leucopus* and *P. maniculatus*. It occasionally appears on other ecologically associated mammals. Class 3. (188).

**Peromyscopsylla scotti* I. Fox.—Our only specimens of this species are from *Peromyscus leucopus*. They are too few, however, to establish a definite host relationship. This flea appears to be very rare in eastern New York, and extensive collections in the Hudson valley have yielded only one locality record. Possibly competition with *P. hesperomys* is a factor in its distribution, or perhaps it is a nest flea which is seldom found upon the host animal. Class 1 or 2. (4).

FAMILY ISCHNOPSYLLIDAE

Nycteriodopsylla chapini Jordan.—This little known and seldom collected flea has been most often taken from the big brown bat, *Eptesicus fuscus*. Our

collection was from a winter roost, and further examination of such roosts might show this species to be more common than past collections indicate. Class 1. (9).

Myodopsylla insignis (Rothschild).—This is a common parasite of the little brown bat, *Myotis lucifugus,* and occurs in great numbers in breeding colonies. It has, however, been taken from other bats in sufficient numbers to indicate that it is not wholly restricted to this one species. Class 2. (100).

REFERENCES

BENTON, ALLEN H. 1955. Notes on some rare or little-known New York Siphonaptera. *Jour. N. Y. Entom. Soc.,* **63**:139-140.

——— AND RICHARD F. KRUG 1956. Mammals and siphonapterous parasites of Rensselaer county, New York. *N. Y. State Museum and Science Service Bulletin* No. 353: 22 pp.

CONNOR, PAUL In Press. Mammals and fleas of Schoharie and Otsego counties, New York. *New York State Museum and Science Service Bulletin.*

CUMMINGS, EDWARD D. 1954. Notes on some Siphonaptera from Albany county, New York. *Jour. N. Y. Entom. Soc.,* **62**:161-165.

FULLER, H. S. 1943. Studies on Siphonaptera of eastern North America. *Bull. Brooklyn Entom. Soc.,* **38**:18-23.

HOLLAND, G. P. 1949. Siphonaptera of Canada. *Dominion of Canada, Dept. of Agr., Tech Bull.,* **70**: 306 pp.

HOPKINS, G. H. E. 1957. Host associations of Siphonaptera. *In* "First Symposium on Host Specificity among Parasites of Vertebrates." Univ. of Neuchatel:64-87.

——— AND MIRIAM ROTHSCHILD 1953. *Catalog of the Rothschild Collection of fleas (Siphonaptera) in the British Museum (Natural History).* Vol. 1, (Tungidae and Publicidae). London. xv and 361 pp.

LAYNE, JAMES N. 1954. The biology of the red squirrel, *Tamiasciurus hudsonicus loquax* (Bangs) in central New York. *Ecol. Monog.,* **24**:227-267.

WELLS, ROGER W. 1957. Host-parasite relations of some small mammals in central New York. M.S. Thesis, State Univ. of New York College of Forestry. 112 pp.

The Distribution, Variation, and Life History of the Frog Cochranella viridissima in Mexico[1]

WILLIAM E. DUELLMAN
Museum of Natural History, University of Kansas, Lawrence

JEROME B. TULECKE
Department of Biology, Wayne State University, Detroit, Michigan

Frogs belonging to the family Centrolenidae first were reported from México by Taylor (1942:74-7), who described *Centrolenella viridissima* from Agua del Obispo, Guerrero, and recorded a specimen of *Centrolenella fleischmanni* from Salto de Agua, Cerro Ovando, Chiapas. An additional specimen of *C. viridissima* was reported by Taylor (1949:12-3) from Río Grande, Oaxaca. Goodnight and Goodnight (1956:146) recorded *C. fleischmanni* from Palenque, Chiapas. Taylor (1951:34) placed both *fleischmanni* and *viridissima* in the genus *Cochranella.*

Field work in México by the senior author in 1956 and by both of us in 1958 has resulted in doubling the number of known specimens of these frogs from that country. Also, life history data were obtained. The purpose of this report is to discuss the variation in, and systematic status of, Mexican centrolenids, to describe the eggs and tadpoles of *C. viridissima,* and to place on record the accumulated locality records for this frog in México.

Acknowledgments.—For the loan of specimens we thank Doris M. Cochran, United States National Museum (USNM);[2] James R. Dixon, College Station, Texas (JRD); Hobart M. Smith, University of Illinois Museum of Natural History (UIMNH); Charles F. Walker, University of Michigan Museum of Zoology (UMMZ), and Richard G. Zweifel, American Museum of Natural History (AMNH).

We are indebted to Ann S. Duellman, Richard E. Etheridge, and John Wellman for their assistance in collecting these elusive frogs and to Priscilla H. Starrett for helpful suggestions. The senior author's field work was made possible by grants from the American Philosophical Society, the National Academy of Sciences, and the Graduate School of Wayne State University, and the generous support of the Museum of Zoology of the University of Michigan.

Variation and Systematic Status

Taylor (1942:75) stated in the diagnosis of *C. viridissima:* "Re-

[1] Contribution No. 46 from the Department of Biology, Wayne State University, Detroit 2, Michigan.

[2] Specimens are cited by catalog number following abbreviations for collections; the private collection of Edward H. Taylor and Hobart M. Smith is abbreviated EHT-HMS.

lated to *C. fleishmanni* [*sic*], but with shorter, stouter limbs and shorter, wider digits; tibiotarsal articulation does not or barely reaches tip of snout while in *fleishmanni* [*sic*] it reaches much beyond." He stated also that in *fleischmanni* the choanae are much larger, there are no fleshy folds below the anus, and the upper parts are smoother. Upon reporting a specimen of *C. viridissima* from Río Grande, Oaxaca, Taylor (1949:13) stated: "*Centrolenella fleischmanni*, also occurring in México, differs in having the second finger much shorter than the first. A white area is present on the eyelids. The leg is distinctly longer, the tibiotarsal joint reaching 2-3 mm beyond the snout tip."

Of six topotypic *viridissima* the tibiotarsal articulation reaches to between the eye and the snout in two, and to the tip of the snout or slightly beyond in four. In 23 *fleischmanni* from Costa Rica (UMMZ 117668-71) the tibiotarsal articulation falls between the anterior corner of the eye and someplace beyond the snout. The relative lengths of the first and second fingers are highly variable in both series. In all, the upper eyelid is white. In specimens of both series there are fleshy folds beside the anus; in some these folds extend below the anus. There is no significant difference in the size of the choanae, nor is there any evident difference in the relative smoothness of the skin on the dorsum.

Nevertheless, there exist certain minor differences between the series of *C. fleischmanni* from Costa Rica and the specimens of *C. viridissima* from Guerrero. In those from Costa Rica the digits of the feet are slightly more robust than those in *viridissima*. All of the *fleischmanni* have scattered chromatophores on the back; these appear in only one of the six topotypes of *viridissima*. In other specimens from México the relative thickness of the digits approximates that in topotypic *viridissima*. About half of the specimens have scattered chromatophores on the dorsum. All Mexican specimens have a silvery white pericardium, which is especially noticeable in living individuals. On the basis of this comparison we tentatively conclude that the existing specimens from México represent a single species, *viridissima*, which we provisionally consider distinct from *fleischmanni* as known in Costa Rica and Nicaragua. Possibly these populations represent a single species or two races of a single species. The exact status of these frogs can be settled only after the acquisition of more specimens, especially from northern Central America, and careful comparison of the living frogs.

Adults of *C. viridissima* from eastern México are slightly larger than those from Agua del Obispo, Guerrero, and show minor differences in proportions of the body (Table I). Because of their poor state of preservation, measurements could not be taken with any degree of accuracy on most of the specimens from Chiapas.

In life these frogs are pale lime green above, sometimes with small scattered cream or pale yellow spots. The feet are yellow, and the vocal sac is white. The skin of the venter is transparent, permitting a view of the silvery white pericardium, of the stomach and intestines, and of the ventral abdominal vein. The iris is light golden (Fig. 1).

TABLE I.—Variation in size and proportions of adult male *Cochranella viridissima* from Veracruz and Guerrero, México (Means are given in parentheses below the observed ranges).

Sample	Number of Specimens	Snout-vent Length	Foot Length / Snout-vent Length	Head Length / Snout-vent Length	Head Width / Snout-vent Length
Veracruz	4	23.9-24.8 (24.5)	.425-.452 (.438)	.243-.251 (.246)	.332-.350 (.341)
Guerrero	5	20.2-21.9 (21.2)	.462-.465 (.464)	.251-.262 (.256)	.347-.366 (.358)

DISTRIBUTION AND ECOLOGY

Recent collecting in México has revealed the presence of *Cochranella viridissima* on the Gulf slopes of the Sierra Madre Oriental as far north as central Veracruz. Also, it has been collected on the Gulf lowlands of Chiapas and in Los Tuxtlas, an isolated volcanic range in southern Veracruz. Thus, the species is known from foothills from central Veracruz and central Guerrero southeastward to the Gulf lowlands of Chiapas and to the Pacific slopes of the Sierra Madre in Oaxaca and Chiapas. Locality records for the 31 Mexican specimens are:

Chiapas: Palenque, UIMNH 11302-3; Río Mala, Unión Juarez, UIMNH 40969; Salto de Agua, Cerro Ovando, USNM 115499; Soconusco, UMMZ 87863. *Guerrero:* Agua del Obispo, EHT-HMS 27719-27 (Taylor, 1942), UMMZ 118584 (6). *Oaxaca:* Cerro Azul, UIMNH 40970; Río Grande, AMNH 51846. *Veracruz:* 3 km. SW of Huatusco, UMMZ 119517; 7 km. ENE of Huatusco, UMMZ 118585; Los Chaneques, 2 km. N of Santiago Tuxtla, UMMZ 115297 (3), 118174 (3); Yanga, JRD 647.

At Los Chaneques in the foothills of Los Tuxtlas these frogs were at an elevation of 350 meters in a small ravine surrounded by remnants of rainforest. Near Huatusco they were at elevations of about 1300 meters along streams in cloud forest on the slopes of the Sierra Madre Oriental. At Agua del Obispo, Guerrero, they were on broad leaf trees along a small stream in open pine-oak forest; this locality lies at an elevation of 900 meters near the crest of a low divide on the Pacific slopes of the Sierra del Sur.

LIFE HISTORY

Breeding choruses of *Cochranella viridissima* have been found on June 28, 1958, at Agua del Obispo, July 17, 1958, near Huatusco, and July 20, 1956 at Los Chaneques. A single male was heard calling at

Los Chaneques on January 25, 1958, and another near Huatusco on January 27, 1958. Males call from leaves of trees over mountain streams. At Agua del Obispo individuals were found 2 to 3 meters above the stream; others were somewhat higher but could not be reached. At Los Chaneques calling males were on leaves of trees overhanging the ravine and small stream; one was on the underside of a vine leaf only about two meters above the water. Near Huatusco they were calling from the tops of trees above rushing mountain streams; at 3 kilometers southwest of Huatusco many frogs were calling from treetops about 20 to 25 meters above the stream. At another locality one was secured from a leaf about 10 meters above the stream.

The call is a single high "peep" usually no more than two or three seconds in duration. Frequently the time-lapse between calls is more than one minute.

At Agua del Obispo, Guerrero, a clutch of 22 eggs was found on June 28, 1958, and another of 29 eggs on July 2, 1958. Both clutches were adherent to the undersides of tree leaves 1 1/2 to 2 meters above the stream. The envelopes of the individual eggs were barely discernible; the entire clutch was covered with jelly (Fig. 1). The jelly was clear, pale green; the yolk was yellow, and the embryos were creamy white. Under magnification, preserved embryos show closely placed chromatophores on the dorsum of the body and on the muscular part of the tail. The embryos showed no particular orientation; some were head down, others, head up. When the leaf was rotated, some

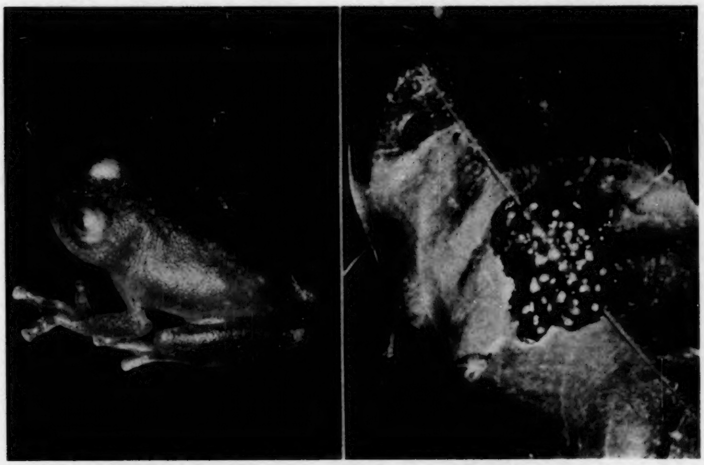


Fig. 1.—Adult and eggs of *Cochranella viridissima* from Agua del Obispo, Guerrero. Left: adult male (approximately twice natural size; actual length 21.9 mm). Right: clutch of eggs on underside of leaf overhanging a stream (approximately one-half natural size).

of the embryos rotated with it, but most retained their original positions.

The leaves with the adherent egg-clutches were collected and suspended above plastic containers. The clutch discovered on June 28 hatched on July 1; that found on July 2 hatched July 6. A hatching tadpole has a body length of 2.9 mm. At the time of hatching, the tadpoles have two partially developed lower tooth rows and the beginning of an upper row.

Two tadpoles six days old have body lengths of 3.1 and 3.4 mm. and total lengths of 10.5 and 11.2 mm. Ten tadpoles eight days old have body lengths from 3.1 to 3.8 (average 3.4) mm and total lengths from 10.4 to 12.6 (average 11.5) mm.

Following is a description of an eight-day old tadpole (UMMZ 118589): In dorsal view the head and body are approximately oval, widest at midbody; eyes one-third distance from snout to end of body and somewhat closer to midline than to lateral outline of head; nostrils midway between eye and snout and somewhat more median than eyes. In lateral aspect, greatest depth of body two-thirds distance from snout to vent; mouth anteroventral; snout protruding beyond mouth; spiracle about three-fourths the distance from snout to vent, below midline, and its opening directed posteriorly; anal tube median and sloping posteroventrally at an angle of about 35 degrees. Tail musculature terminating in a point immediately anterior to tip of tail; greatest depth of tail musculature slightly more than one-half greatest depth of tail; tail fin relatively narrow and rounded posteriorly. In preservative, tail musculature and body pale cream, with scattered chromatophores on dorsal surface; tail fin transparent (Fig. 2).

Tooth rows 2-2; second upper tooth row present only laterally; lower tooth rows slightly longer than upper ones, complete and wavy. Lips only slightly differentiated, edges scalloped, and not forming a distinct sucker. A row of relatively large papillae around mouth; a slight fold of the lips at lateral corners of mouth. Upper horny beak forming a broad arch, not indented medially; lower beak heavier and forming a narrower arch (Fig. 3).

In comparison with tadpoles of *C. fleischmanni* of approximately the same size from Costa Rica (UMMZ 118658), the following differences are noted: *fleischmanni* has a somewhat more blunt snout in lateral view, mouth directed more ventrally, three well-developed lower

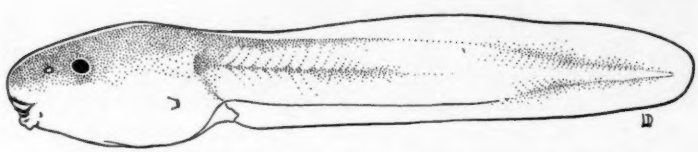


Fig. 2.—Eight-day old tadpole of *Cochranella viridissima* (UMMZ 118589); x 8, actual length 12.6 mm.

Fig. 3.—Mouth parts of eight-day old tadpole of *Cochranella viridissima* (UMMZ 118589); x 50.

tooth rows, and upper beak indented medially. Tadpoles of *C. granulosa* (UMMZ 118660) and *C. talamancae* (UMMZ 118657), both from Costa Rica, differ from *viridissima* in having proportionately longer and narrower bodies, longer tails with narrower fins, mouth large and sucker-like, and upper beak indented medially.

Three metamorphosing individuals were found sitting on herbaceous vegetation along a small stream at Los Chaneques on January 25, 1958. They have snout-vent lengths of 11.6, 12.3 and 12.5 mm. Only a stub of the tail remains on each; the mouth has not completely expanded. In life they were pale green.

REFERENCES

GOODNIGHT, CLARENCE J. AND MARIE L. GOODNIGHT 1956. Some observations in a tropical rain forest in Chiapas, Mexico. *Ecology*, **37**(1):139-150.

TAYLOR, EDWARD H. 1942. New tailless amphibia from Mexico. *Univ. Kansas Sci. Bull.*, **28**(5):67-89.

———1949. New or unusual Mexican amphibians. *Amer. Mus. Novitates*, **1437**:1-21.

———1951. Two new genera and a new family of tropical American frogs. *Proc. Biol. Soc. Wash.*, **64**:33-40.

Home Range, Reproduction, and Foods of the Swamp Rabbit in Missouri

J. E. TOLL,[1] T. S. BASKETT,[2] and C. H. CONAWAY[3]

In Missouri, the swamp rabbit (*Sylvilagus aquaticus* (Bachman)) occurs principally in the southeastern lowlands. It is a locally abundant and popular game animal. Relatively little is known of the life history of this species, particularly in the northern part of its range. The object of this study is to contribute to our knowledge of specific aspects of the life history of this species.

The study area was in Mingo swamp which lies in Stoddard, Wayne, and Bollinger counties, in an abandoned valley of the Mississippi River. The swamp formerly supported extensive stands of bald cypress (*Taxodium distichum*), tupelo gum (*Nyssa aquatica*) and several species of oaks. Drainage, logging, and clearing of the higher land for farms have greatly altered the landscape. But large acreages of good swamp rabbit habitat remain in cut-over lowland hardwood types, particularly on the Mingo National Wildlife Refuge and the Duck Creek Wildlife Area.

This paper is a contribution from the Missouri Cooperative Wildlife Research Unit and the Department of Zoology, University of Missouri. The senior author was an Edward K. Love Fellow. We are indebted to Howard M. Wight, Missouri Conservation Commission, for valued suggestions and assistance; and to G. K. Brakhage and L. J. Schoonover for facilities and assistance.

Home Ranges

The trapping area.—Sizes of home ranges were determined both by trapping and by beagle chases. These operations were carried out on a portion of the Duck Creek Wildlife Area. The trapping area comprised 72 acres, extending from the edge of a shallow impoundment on the south to higher dry land on the north (Fig. 1). This was a logged-over hardwood site; pin oaks (*Quercus palustris*) and overcup oaks (*Q. lyrata*) dominated. Overstory trees seven to ten inches dbh were most common. Stand density varied from about 95 overstory trees per acre to openings with only 15 per acre; in these openings there was an undergrowth of blackberries (*Rubus sp.*) and other small shrubs. The north and west sides of the area were bordered by a road with a grassy right-of-way about 70 yards wide.

---

[1] Crab Orchard National Wildlife Refuge, U. S. Bureau of Sport Fisheries and Wildlife, Carterville, Illinois.

[2] Missouri Cooperative Wildlife Research Unit, University of Missouri, Columbia.

[3] Department of Zoology, University of Missouri, Columbia.

Trapping and tagging procedure.—The trapping area was divided into 72 one-acre squares. A trap was placed at the center of each square, making a grid nine traps deep and eight wide; traps were 70 yards apart. Box traps operated with a treadle were used. Various types of bait were used, but unbaited traps were as successful as baited ones.

Trapped rabbits were weighed, sexed, measured, tagged, and released at the point of capture. Recaptured rabbits were recorded and released.

Two types of tags were used. One was a small numbered aluminum poultry tag attached to the ear with crimping pliers. Cottontails (*Sylvilagus floridanus*) were marked with this tag only. The alumi-

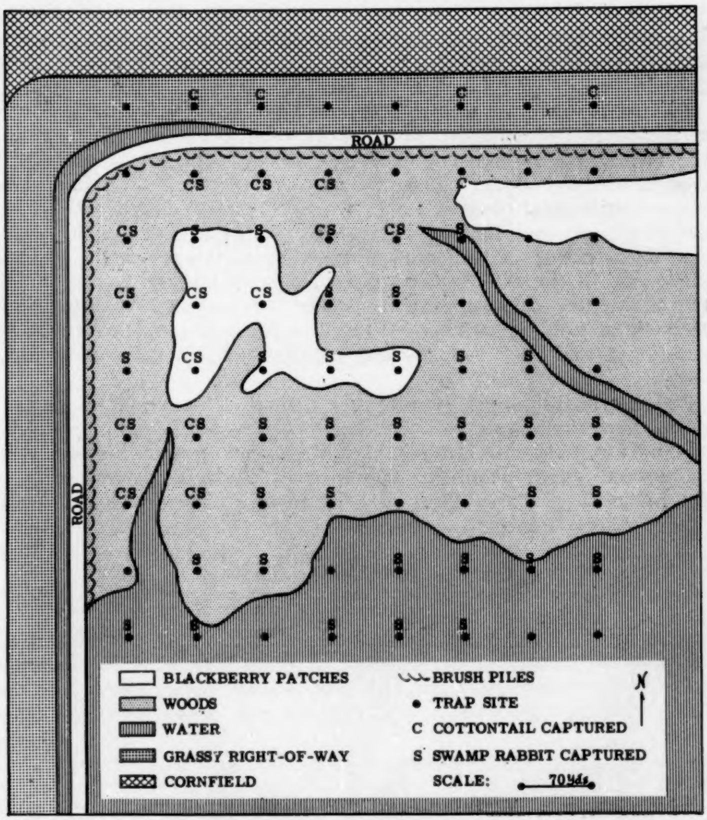


Fig. 1.—The trapping area.

num tag was placed in the ear of swamp rabbits (*S. aquaticus*), and a laminated plastic tag was attached to the other ear. The plastic tags were round or square, about one inch across, and were made of pieces of colored acetate plastic 0.015 to 0.020 inches thick. They were assembled in various color combinations and designs so that each rabbit could be identified individually. Plastic tags were attached to the ear by rabbit ear tags procured from National Band and Tag Company. None of the poultry tags was known to be lost, and the one plastic tag known to be lost came off when the rabbit was confined in a trap. With 7 × 50 binoculars, rabbits could be identified by the plastic tags as far away as 75 yards; since there were few openings of that length, the tags were generally satisfactory for the area.

Trapping results.—Traps were set for short periods starting in June, 1956; however, success was too low to warrant full-time trapping until November (Table I). Between November 15, 1956, and February 16, 1957, the traps were in constant operation.

During November most of the trap sites were on dry land. Water levels rose in December reaching a peak about the 18th. At that time the water boundaries were as shown on the map (Fig. 1), and although the traps were placed on logs or other dry situations, most traps in the southernmost two rows were surrounded by water. As the water encroached, trapping success diminished, and when water depth reached about six inches no more captures were made. During the period of trapping, 35 swamp rabbits were trapped a total of 143 times. Twenty-one of these rabbits were trapped at least three times each. The greatest number of captures for a single female was 16 and for a male, 8. Twenty-eight (80%) were captured more than once.

Eighteen cottontails were caught a total of 35 times. Recapture rates were much lower than those for the swamp rabbit. Only six of the cottontails were recaptured, and only one cottontail was caught more than three times. No attempt was made to estimate sizes of the home ranges of cottontails because of the low recapture rate,

TABLE I.—Monthly trapping success

Month	Trap nights	Captures of swamp rabbits	Captures of cottontails
June	60	0	0
July	224	3	0
August	336	0	0
September	432	2	0
October	0	....	....
November	720	40	11
December	1360	43	13
January	1800	39	10
February	1050	16	1

which may have indicated movement in and out of the trapping area.

Both Calhoun (1941) and Lowe (1958) indicated rather sharp delineation of swamp rabbit and cottontail ranges where both species occurred. In the present study, a gradation from cottontail to swamp rabbit ranges with a band of overlap, occurred within the trapping area (Fig. 1). Only cottontails were caught in the grassy right-of-way at the north end of the trapping plot. Both species were captured in a belt 70 to 140 yards wide bordering a road, and only swamp rabbits were caught deep in the wooded swamp. Cottontails were usually trapped farther from open water than were swamp rabbits but there were exceptions. In general, the cottontails were taken closer to the fields, road strips, and brush piles, but a considerable portion of the trapping area was tenable for both species.

Calculation of home ranges from trapping data.—Two systems for calculating areas in home ranges from trapping data were used. The first was to determine "minimum home ranges" as described by Mohr (1947): areas enclosed by lines connecting the outside points of capture for each rabbit were determined by planimeter. The second system involved the addition of "trap squares" as described by Haugen (1952). According to this system, which is one of several designed to add boundary strips, each trap within the grid is presumed to represent a square area extending halfway to the next trap; a home range is computed by adding "trap squares" in which the rabbit was trapped, plus any intervening squares.

Average home range sizes were computed only for swamp rabbits trapped four times or more; the choice of this figure was arbitrary. Results for these selected individuals are shown in Table II. Home ranges for seven females averaged 5.9 acres when computed by the "trap squares" method, and 2.1 acres when computed by Mohr's "minimum home range" procedure. Home ranges of seven males averaged 4.6 acres ("trap squares") and those of five males averaged 1.8 acres ("minimum home range"). Most investigators have found home ranges of male cottontails to be larger than those of females (Dalke, 1942; Bruna, 1952). In our study of swamp rabbits, results both of trapping and of beagle chases indicated that the females had the larger home ranges. Our data were gathered when there was little or no breeding.

Beagle chase procedure.—Most of the recorded chases of tagged rabbits by beagles were made in January and February. All recorded chases were made on the trapping area described previously. During most successful chases the observer was aided by one or two other persons.

When a chase was started one person stayed at the point of origin and tried to identify the rabbit by its ear tag when the rabbit returned. Many times the rabbit was identified when flushed and its identity checked upon its return.

TABLE II.—Home ranges of swamp rabbits trapped at least four times

Tag no.	No. of captures	No. of beagle chases	Sizes of home range in acres according to: "trap squares"	"minimum home range"	beagle chases	Maximum diameter of home range in yards derived from: trapping	beagle chases	both	Greatest departure of beagle chase from "minimum home range" (yards)
FEMALES									
409	16	3	8.0	4.0	4.6	210	234	242	84
414	13	3	9.0	3.5	3.5	284	280	350	79
450	11	2	7.0	2.5	5.5	219	263	263	84
418	9	2	6.0	2.0	3.4	219	238	252	46
460	6	2	4.0	1.0	2.5	219	284	284	89
406	6	..	4.0	1.0	....	140	......	......	....
430	5	3	3.0	1.0	5.0	156	298	298	130
Averages			5.9	2.1	4.1	208	266	282	85
MALES									
444	8	..	7.0	2.4	....	280	......	......	....
425	6	..	5.0	1.5	....	159	......	......	....
441	5	1	4.0	....	1.9	210	140	215	93
417	4	3	4.0	2.0	2.6	158	200	205	93
413	4	1	6.0	2.0	1.7	280	130	280	24
442	4	2	4.0	1.0	1.6	196	163	233	82
415	4	..	2.0	....	....	98	......	......	....
Averages			4.6	1.8	2.0	197	158	233	73

One person followed closely behind the dogs, and marked the trail with tissue paper. Routes were retraced and recorded when the chase was over. The paper was picked up to avoid confusion on

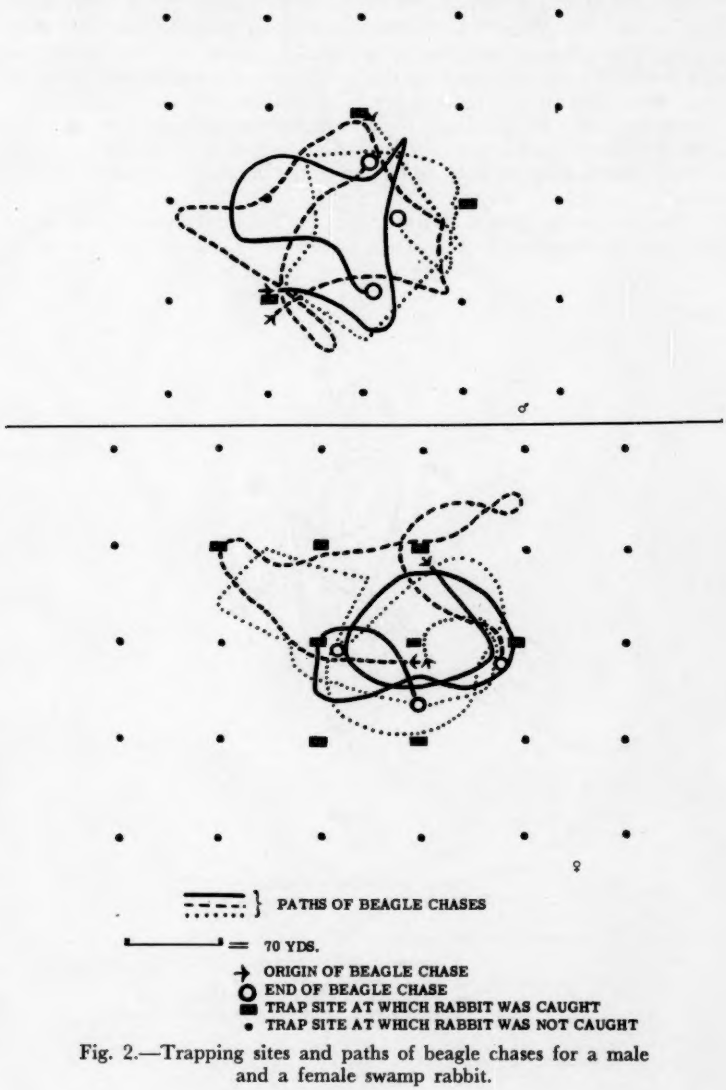


Fig. 2.—Trapping sites and paths of beagle chases for a male and a female swamp rabbit.

subsequent runs. Beagle chases were not recorded if the identity of the rabbit was uncertain, or if the dogs lost the trail for an extended period and the rabbit's identity could not then be rechecked.

Results of beagle chases.—A total of 29 chases of 15 individuals was made. Of these 15 rabbits, nine were females and six were males. The greatest number of acceptable chases of any individual was three. The route taken by the rabbit was plotted to scale and the area calculated with a planimeter. The maximum home range determined by this method was 5.5 acres for a female and 7.9 acres for a male. These ranges are much smaller than those reported by Lowe (1958) for swamp rabbits in Georgia; the latter averaged about 19 acres.

The similarity in the routes taken by the same animals on separate runs is apparent in Figures 2, 3, and 4. These figures also show

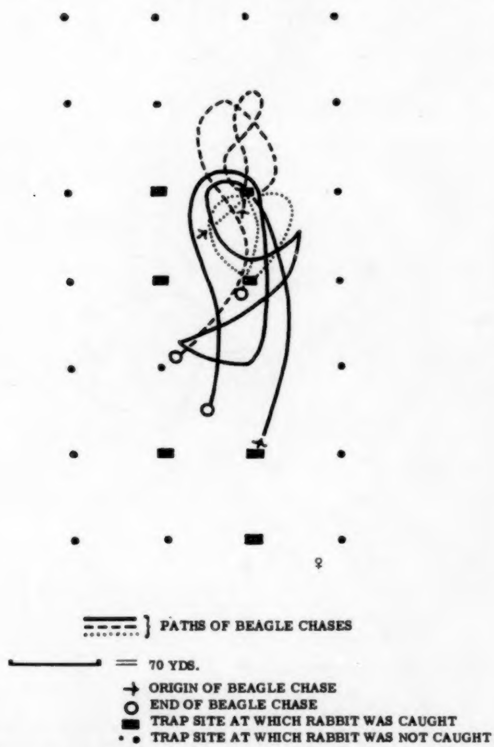


Fig. 3.—Trapping sites and paths of beagle chases for a female swamp rabbit.

the close correspondence between successful trap sites and the routes taken during beagle chases. Another expression of this correspondence is the fact that the greatest departure of a beagle chase from the "minimum home range" for a rabbit trapped four or more times was 130 yards. This information, as well as a summary of home range

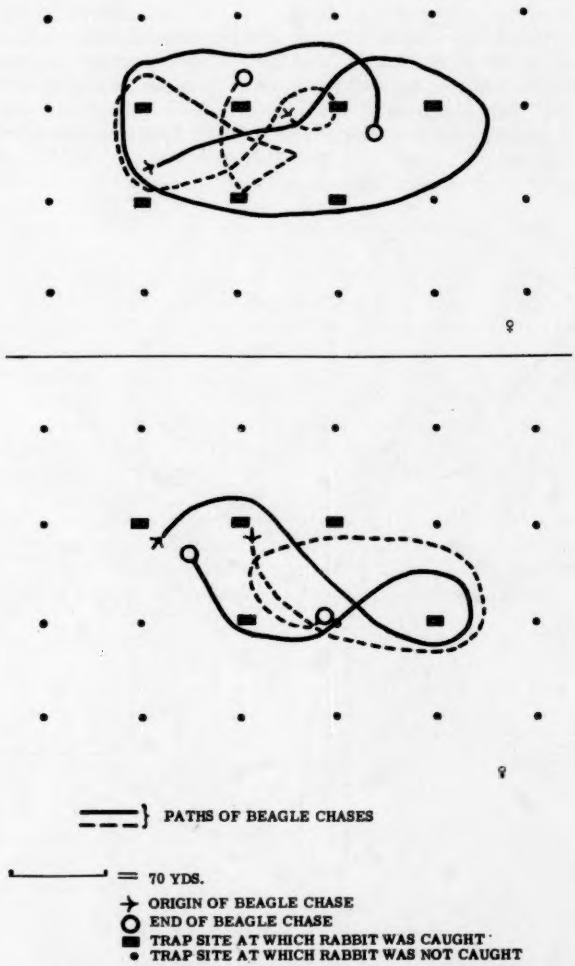


Fig. 4.—Trapping sites and paths of beagle chases for two female swamp rabbits.

sizes as determined by several methods for rabbits trapped four or more times is shown in Table II. Included in the table are measures of "maximum diameters" or the greatest distance between any points in an indicated home range.

Overlapping ranges.—The great extent of overlapping of home ranges is illustrated in Figure 5 where home ranges of 11 males, determined by trapping and beagle chases, are plotted in spatial relationship. Home ranges of the females overlapped similarly, and those of males and females overlapped one another. Lowe (1958) thought that home ranges of the swamp rabbits in Georgia overlapped but little. The density of his swamp rabbit population was much lower than ours (about one rabbit per 18 acres on his area *vs* one per 1.5 acres on ours), and this fact may help explain the greater overlapping and smaller home ranges we found.

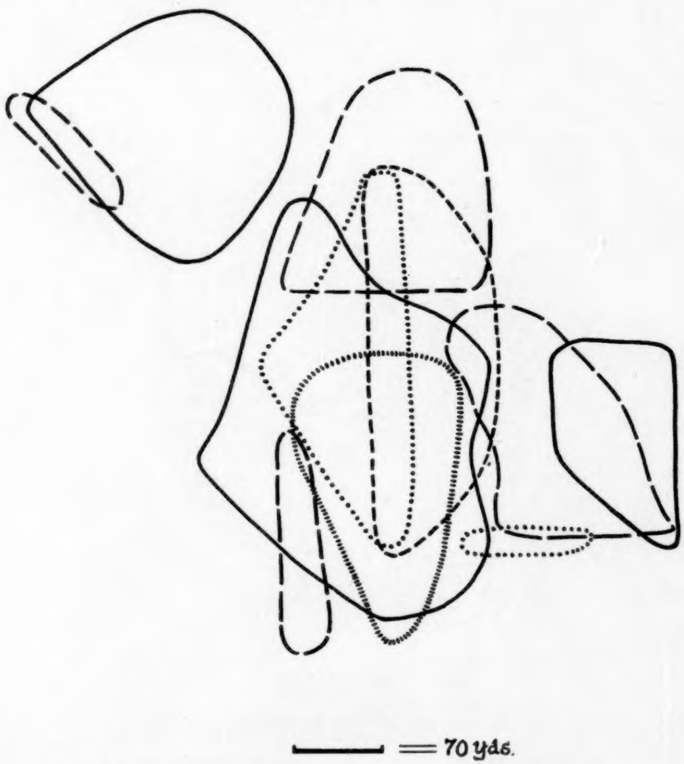


Fig. 5.—Overlapping home ranges of 11 male swamp rabbits.

Beagle chases as a means of determining home ranges.—Chasing by dogs has been used to give some information about sizes of home ranges of the marsh rabbit (*Sylvilagus palustris*) by Carr (1939) and for the swamp rabbit by Lowe (1958). However, neither of these workers gathered detailed information about individually-marked rabbits by chasing with dogs, and the data they secured were not related to trapping records.

The adequacy of beagle chases in determining size of home ranges is worthy of discussion. One might wonder how often in the course of a chase the beagle shifted to a different rabbit. In our study this could have happened rarely, if at all, because: (1) during several chases rabbits were individually identified more than once, and (2) whenever there was real doubt about this point, the record of the chase was discarded.

A second question is whether paths of beagle chases really represent home ranges, even when accurately mapped. This question cannot be answered categorically, but the fact that the rabbits usually return to the point of origin of the chase implies that they tend to remain within a familiar area. Howard M. Wight (Pers. Comm.) has observed cottontails that were released several miles from their home ranges running in a straight line when chased by a dog. Thus a rabbit pushed out of its home range might run in a straight line and the pattern of the chase would be quite different from those shown in Figures 2-4. Further, beagles of the type we used are often far behind the rabbit. During a chase, rabbits were sometimes seen to stop and lick themselves in leisurely fashion. It is hard to imagine that under such circumstances the animal is being pushed out of its home range. Additional evidence that beagle chases accurately estimate home ranges is provided by the correspondence between the successful trapping sites and the area enclosed by beagle chases, as well as the similarity of areas enclosed by different chases of the same rabbit.

In evaluating the "trap squares" method and the "minimum home range," Hayne (1949) noted that the critics of the "trap squares" approach believe that it gives an estimate that is too large, and critics of the "minimum home range" think that it gives an estimate that is too small (Hayne, 1949; Stickel, 1954). Interestingly, in six of nine cases, the estimated size of home range obtained by beagle chases fell between the sizes obtained using the other two methods.

One advantage of determining home ranges by beagle chases is the rapidity of the method; another is the simplicity of determining and expressing results.

REPRODUCTIVE HISTORY

Onset of breeding season.—The start of the reproductive season in cottontails is controlled by the breeding condition of the female, for as Hamilton (1940) pointed out, the male is capable of breeding

before the female and remains fertile after the female is no longer in breeding condition. In Texas, Hunt (1959) found that some individuals of both sexes of swamp rabbits were in breeding condition throughout the year, but reproductive activity diminished in the fall.

In Missouri it appears that a definite anestrous period may occur since no adult female collected between November and the end of January was reproductively active. A pre-estrous female was taken February 25, 1957, and two more pre-estrous animals were taken March 9, 1957. On March 16, 1957, a recently post-partum female in full lactation was collected. Back-dating 40 days (an average of Hunt's estimated gestation period, for the swamp rabbit), February 4 was estimated as the conception date. Similarly five more females were estimated to have been bred during February. Collections were not sufficient to determine the month when breeding activity terminated, but this apparently occurs by late summer.

Breeding condition in males.—Testes were preserved from some males during each month, October, 1956, through June, 1957. Histological sections were prepared from one testis and cauda epididymis of each male. If sperm was found in the testis and the tail of the epididymis, the rabbit was considered to be in breeding condition. Material from 42 animals was analyzed.

Since no collections were made during August and September, the reproductive status through this period is unknown. In October four males were collected and only one of these was in breeding condition. During November three adult males were collected. One of these had no sperm in either the testis or epididymis while the other two showed active spermatogenesis. Three of the five males taken during December were producing sperm while two (one adult and one young) had no stages later than secondary spermatocytes in the testes. All animals taken throughout spring and early summer were reproductively active.

Some male swamp rabbits in Missouri populations may be in breeding condition every month of the year. Because no collections were made in the late summer this statement cannot be supported with direct evidence. Probably the number of breeding males begins to decline during the late summer and remains low through November. By the end of December both juvenile and adult males are in breeding condition.

The testes of reproductively active swamp rabbits are conspicuously smaller than those of breeding cottontails as Layne (1958) has noted. The average weight of both testes from 10 Missouri cottontails taken in March was 21.5 grams while the average weight for both testes from 10 swamp rabbits taken in March was 3.9 grams.

Litter size.—Litter size was estimated by three methods. The first was to count the corpora lutea of all swamp rabbits collected between March 16 and June 23, 1957. Forty-six females had an average corpora lutea count of 3.7 (range 2-6). These figures indicate maxi-

mum litter size and would not account for post- or pre-implantation losses.

The second approach was to count the embryos found in the pregnant females. Only embryos having a crown-rump measurement of 35 mm or more were included. Excluding embryos of small size lessens the error introduced by resorptions occurring in later pregnancy. Embryos in 14 females were counted; half of them had 3 embryos and the average was 2.8 (range 1 to 4). When 24 females with embryos of all sizes were included, the average litter size was 3. Hunt's (1959) embryo counts averaged 2.8 (range 1 to 5) for 29 female swamp rabbits. Svihla's (1929) embryo counts averaged 3.7 (range 3 to 5).

The last approach was counting placental scars. Those counted were probably not more than two weeks post-partum. The average placental scar count in 7 rabbits was 3.4 (range 3 to 4). Conaway (1955) showed that in rats the placental scars formed at the sites of resorbed embryos were indistinguishable from those formed at the sites of term embryos. If this is also true in the swamp rabbit, the placental scar method would result in an overestimation of litter size.

FOOD HABITS

The plant most commonly eaten by swamp rabbits was *Carex lupulina,* locally called swamp grass. This plant is abundant throughout the study area and is used by swamp rabbits from spring until mid-winter. During the same period large amounts of hazelnut (*Corylus sp.*) shoots were eaten. After the *Carex* died-back in late December or early January, swamp rabbits began eating twigs and bark of woody plants. The four most-used plants during the late winter months were blackberry (*Rubus spp.*), hazelnut, deciduous holly (*Ilex decidua*), and spice bush (*Lindera benzoin*).

Table III lists plants used, time of usage, and a coarse measure of abundance of plants. Care was taken to record plants only in the area used by the swamp rabbits and not used by cottontails.

During a two-month period of flooding in spring, 1957, swamp rabbits were forced on to roadways running through the Mingo Refuge. They ate Alta fescue, winter wheat, and sericea lespedeza (*L. cuneata*).

In other areas, swamp rabbits are reported to eat a wide variety of grasses, sedges, forbs, and barks and shoots of trees (Svihla, 1929; Smith, 1940; Calhoun, 1941).

Coprophagy.—Soft pellets occurred frequently in the stomachs of the swamp rabbits and cottontails that were collected. During the later part of the study all rabbits collected were examined for soft feces in the stomach and rectum. Information obtained was recorded in hourly intervals (Fig. 6). These small samples indicate that coprophagy occurs mainly during the daylight hours when the rabbits are resting, and not at night, when they are feeding. This is the pat-

TABLE III.—Plants used as food by swamp rabbits

Species	Amount of usage	Season used	Abundance of plant
Sedge (*Carex lupulina*)	heavy	spring summer, fall & early winter	very common
Blackberry (*Rubus* spp.)	heavy	fall & winter	very common
Hazelnut (*Corylus* sp.)	heavy	fall & winter	very common
Deciduous holly (*Ilex decidua*)	heavy	winter	common
Spice bush (*Lindera benzoin*)	heavy	winter	common
Hackberry (*Celtis laevigata*)	medium	winter	common
Sumac (*Rhus aromatica*)	medium	winter	common
Sassafras (*Sassafras albidum*)	medium	winter	rare
Trumpet vine (*Campsis radicans*)	light	winter	very common
Hercules club (*Aralia spinosa*)	light	winter	common
Overcup oak (*Quercus lyrata*)	light	winter	common
Pin oak (*Quercus palustris*)	light	winter	very common
Elm (*Ulmus americana*)	light	winter	common
Elm (*Ulmus rubra*)	light	winter	common
Cherry bark oak (*Quercus falcata* var. *pagodaefolia*)	light	winter	common
Hickory (*Carya* spp.)	light	winter	common
Green brier (*Smilax* spp.)	light	winter	common
Paw paw (*Asimina triloba*)	light	winter	rare

tern observed in the jack rabbit by Lechleitner (1957). Layne (1958) has also reported coprophagy in the swamp rabbit.

SUMMARY

1. Thirty-five swamp rabbits were trapped 143 times on a 72-acre area. Traps were located in a grid pattern, 70 yards apart. All rabbits were tagged with colored plastic tags which made field identification of individuals possible.

2. Home ranges for females trapped four times or more averaged 5.9 acres when computed by addition of "trap squares," and 2.1 acres when determined by the "minimum home range" method. Corresponding figures for males were 4.6 and 1.8 acres.

3. Sizes of home ranges were also estimated by chasing individually tagged rabbits with beagles, and recording the paths of the chases. Home ranges determined in this fashion averaged 4.1 acres for females and 2.0 acres for males. Routes taken by rabbits during beagle chases correspond very closely with trapping records for the same individuals, and with routes taken by the same rabbits in different chases. Beagle chases appear to have much promise for determining home ranges of rabbits. Data can be gathered rapidly and

interpretation is simple. Evidence for the validity of this method is (1) that in six of nine cases the estimated size of home range obtained by beagle chases fell between the home range sizes estimated by "trap squares" and "minimum home ranges; (2) that successive chases of the same animal encompassed similar areas.

4. Female swamp rabbits in southeast Missouri were probably in estrus by early February, and only one female was found reproductively inactive after February 25. No females collected from October through January were in breeding condition. Males attain breeding condition before the females and remain in it longer. Some male swamp rabbits probably are capable of breeding throughout the year.

5. Litter sizes were estimated from corpora lutea counts, embryo counts, and placental scar counts. From corpora lutea counts, the average was 3.7 (range 2 to 6). From embryo counts, the average was 2.8 (range 1 to 4). From placental scar counts the average was 3.4 (range 3 to 4).

6. The plant most commonly eaten by the swamp rabbit was *Carex lupulina*. This plant was eaten until late winter, when it was no longer green. The four most-used plants during the late winter months were blackberry, hazelnut, deciduous holly, and spice bush.

7. Coprophagy was found to be practiced regularly by both swamp rabbits and cottontails. Coprophagy seemed to occur in the daytime during the resting period, and was discontinued at night during feeding.

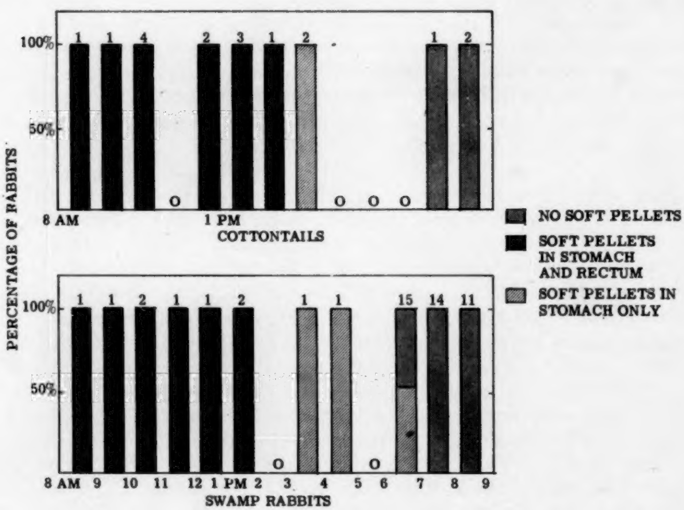


Fig. 6.—Percentages of cottontails and swamp rabbits containing soft pellets.

References

BRUNA, J. F. 1952. *Kentucky Rabbit Investigations.* Dept. of Fish and Wildl. Resources, Frankfort, Ky. 83 pp.

CALHOUN, J. B. 1941. Distribution and food habits of mammals in the vicinity of Reelfoot Biological Station. *Jour. Tenn. Acad. Sci.,* **6**:177-185; 207-225.

CARR, A. F., JR. 1939. Notes on escape behavior in the Florida marsh rabbit. *Jour. Mamm.,* **20**:322-325.

CONAWAY, C. H. 1955. Embryo resorption and placental scar formation in the rat. *Ibid.,* **36**:516-532.

DALKE, P. D. 1942. The cottontail rabbits in Connecticut. *Geol. and Nat. Hist. Surv. Bull.,* **65**:1-97.

HAMILTON, W. J., JR. 1940. Breeding habits of the cottontail rabbit in New York State. *Jour. Mamm.,* **21**:8-11.

HAUGEN, A. O. 1942. Home range of the cottontail rabbit. *Ecology,* **23**:354-367.

HAYNE, D. W. 1949. Calculation of size of home range. *Jour. Mamm.,* **30**:1-18.

HUNT, T. P. 1959. Breeding habits of the swamp rabbit with notes on its life history. *Jour. Mamm.,* **40**:82-91.

LAYNE, J. N. 1958. Notes on mammals of southern Illinois. *Amer. Midl. Nat.,* **60**:219-254.

LECHLEITNER, R. R. 1957. Reingestion in the black-tailed jack rabbit. *Jour. Mamm.,* **38**:481-485.

LOWE, C. E. 1958. Ecology of the swamp rabbit in Georgia. *Ibid.,* **39**:116-127.

MOHR, C. O. 1947. Table of equivalent populations of North American small mammals. *Amer. Midl. Nat.,* **27**:223-249.

SMITH, C. C. 1940. Notes on the food and parasites of the rabbits of a lowland area in Oklahoma. *Jour. Wildl. Mgmt.,* **4**:429-431.

STICKEL, L. F. 1954. A comparison of certain methods of measuring ranges of small mammals. *Jour. Mamm.,* **35**:1-15.

SVIHLA, R. D. 1929. Habits of *Sylvilagus aquaticus littoralis. Ibid.,* **10**:315-319.

Notes on the Following Response and Other Behavior of Young Gray Squirrels

JACK P. HAILMAN[1]

In spite of the fact that a prodigious number of papers on the gray squirrel, *Sciurus carolinensis,* have been published (see bibliography of Flyger, 1951), little is known about the behavior of the young after leaving the nest. This paper presents some preliminary observations on young gray squirrels during the post-nest period, and describes for the first time the "following response" of this species.

Observations

On May 23, 1958, on the grounds of Harvard University, Cambridge, Massachusetts, I saw two squirrels foraging together on the ground; the seemingly peculiar behavior of one drew my attention. This individual approached the other and nuzzled its flanks and shoulder region at intervals of 10-20 seconds. It soon became apparent that this was a young squirrel, as evidenced by its slightly browner coat, smaller body, and relatively larger head, and by the fact that it was following an adult, presumably its mother. This nuzzling behavior continued as they moved across the grass, the young coming to the adult whenever they passed. When the two approached to within six feet of a tree, the young animal broke company and ran to the tree, leaping about a foot up its side in the usual *Sciurus* manner. Here it paused, clinging, and looked toward the adult, which made no detectable noises or movements. The young squirrel then bounded back to the adult and again began vigorously sniffing the shoulder area of the parent. A passing automobile frightened both individuals and the observations were terminated.

The second incident took place on June 2nd in a different part of the Harvard campus. An adult, followed by three young, descended a tree head-first. The young executed the same sniffing motions observed above. Each time the female stopped, the young squirrels moved in and sniffed her back and sides, pushing each other aside. This behavior continued when they reached the ground, and throughout the observations described below. No "play," as such, was observed in the animals, although they often scrambled over one another on the ground in order to keep close to the female. The adult hopped to a nearby fence, which she climbed easily. The first young squirrel to follow was clumsy, but successful, and immediately went to the adult and sniffed her sides. The second young animal to attempt the ascent fell twice from the half-way point, and gave up. The third individual, continually watching the adult, did not try to climb the fence. About a minute later,

[1] Present address: 4401 Gladwyne Drive, Bethesda, Maryland.

the adult and the first young animal rejoined the other two on the ground; the group began foraging across the grass together, with the three young squirrels intermittantly sniffing the female.

One young squirrel became separated from the rest, and began picking up and manipulating items in the grass, including a small stone. The animal was frightened by another person, and leapt onto a nearby basement window pane from which it fell. Later, the squirrel climbed a tree, and observations ceased.

Several groups of gray squirrels were observed on April 25, 1959, in the Municipal Gardens at Norfolk, Virginia. The first group consisted of two young and an adult. Upon my approach, they congregated in the same tree and began to climb upward. As my wife and I arrived at the base of this tree, the young squirrels began to move through the tree tops in separate directions. For a moment or two the adult chattered at me, but then ceased and also began moving away through the trees. I followed one of the young squirrels to study how it climbed and jumped. The woods in this area consisted of various deciduous species, chiefly oaks, and the squirrel climbed to a height of roughly forty feet. The animal was quite agile at climbing and moving along limbs, but was inexperienced in executing leaps from one tree to another. It often hesitated before jumping, and twice, after pausing, it did not jump, but ran back toward the trunk and then out another limb.

Twice again that day we saw groups of squirrels, once with three young, the other time with four, but no adults were with these groups. Although no detailed notes were taken on these latter groups, all the young of these groups appeared to be quite agile at climbing and leaping.

DISCUSSION

DEPENDENCY PERIOD

The time during which the young follow and forage with the mother I have designated as the "dependency period," to correspond with the terminology used for the analogous period in birds (Brackbill, 1953). Tentatively, this period is defined for squirrels as extending from the time when the young leave the nest initially until they are no longer dependent upon the mother (or any adult squirrel) for food or protection. The dependency period is probably a time of transition during which the young squirrel adjusts to life outside the nest. Since bands of young may be seen in the fall and winter (Shorten, 1954:116-117; Flyger, 1955), it is probable that family ties are not completely severed until the first spring of life, at least in some cases, although the amount of dependency, if any, upon the parent during this time is unknown. The fact that the male may sometimes take over the raising of the first litter when the female becomes pregnant with the second (Shorten, 1954) also complicates the delineation of the dependency period. However, the original definition offered above is adequate for purposes of this paper, and may later be refined.

Standard life history references (e.g., Seton, 1928; Hamilton, 1943; and Burt, 1943, 1957) all omit any description of behavior during the dependency period of the gray squirrel. Shorten (1954:137-138) merely mentions that upon leaving the nest, young follow the mother. I discuss below some new questions and problems raised by my observations on young squirrels, and comment on the development of certain behavior patterns during the dependency period.

FOLLOWING RESPONSE AND IMPRINTING

Many young animals are known to follow their parents upon leaving the nest (Thorpe, 1956:397), but there are few careful descriptions of the "following response" in mammalian species. The observations above indicate that the young gray squirrels rely heavily on olfactory clues of the parent, as evidenced by their continual sniffing. A cursory search of the literature indicates that the badger (*Meles meles*) is the only animal in which the young are known to sniff frequently during following (Neal, 1958:35). Young birds react primarily to visual and auditory stimuli while following (Thorpe, 1956:116, 357ff).

It seems quite likely that an olfactory basis for the recognition of the mother is advantageous to young squirrels inside the nest for several reasons: (1) the eyes do not open until the 36th day (Burt, 1957:102); (2) even after the eyes are open, darkness hinders formation of visual recognition, especially in nest-holes. We know that adult squirrels maintain a dominance hierarchy where each individual recognizes all others at distances which seem to preclude good olfactory discrimination (Flyger, 1955). Furthermore, the species' social communicative behavior (or "ritualized" signal behavior) seems to depend largely on visual and auditory signs (Flyger, *ibid.*). It is known also that the gray squirrel is quite dependent upon its visual sense in general behavior (Yoakum, 1902), and that this species has a poorly developed olfactory sense compared to other sciurids (McClelland, 1948), at least as adults. Therefore, the problem of transition from nest life olfactory recognition to adult visual (and auditory) recognition seems to be an important one in the animal's life.

During the following response both olfactory and visual stimuli seem to be important in the parent-young bond, and this may well be the period of transition from one to the other. It is possible that a very rapid emphatic learning, such as "imprinting," occurs at this time, or, on the other hand, that the transition is a gradual one. Imprinting is the term applied to the rapid process by which young birds (and other animals) learn the recognition characters of their species while following the parent (Thorpe, 1956:115-117, 357-367). Imprinting has been reported for many mammals (Thorpe, 1956:397), and probably even exists to some extent in humans (Bowlby, 1953). That young squirrels may become imprinted with the visual recognition characters of their parents during the following behavior seems possible.

It is tempting to think of the olfactory to visual ontogenetic changes

as recapitulating the phylogeny of nocturnal ground dwelling animals dependent primarily upon smell as chief sensory input to the diurnal, arboreal gray squirrel dependent on its visual acuity as the basis of behavior. Perhaps this oversimplifies the problem, but there seem to be selective advantages in retaining olfaction: (1) its use in the nest, as discussed above; (2) its possible advantage in the following response, discussed below under "locomotion and foraging."

Experience during the following period is also thought to affect later sexual behavior of the individual (Thorpe, 1956), although the exact relationship involved is not yet clear. Flyger (1955) notes that the sexual behavior of the gray squirrel is strongly dependent upon certain olfactory clues, and there could exist a connection between this and early olfactory experience.

LOCOMOTION AND FORAGING

The actual motions of climbing, running, jumping, etc., seemed well-developed in all young gray squirrels. Young will cling to, and apparently climb, a tree before their eyes are opened (Smith, 1947); this seems to indicate that these motions develop largely independent from any individual experience. Apparently the young squirrel learns during the dependency period how to use its motor patterns; it learns: (a) which vertical surfaces are climbable; (b) how to choose limbs to jump from one tree to another; and (c) how to choose footholds in climbing difficult objects, such as a board fence. The partial dependence upon olfactory stimuli while following the mother necessitates that the young squirrels stay close to the mother. This, in turn, not only provides better protection to the young but also may encourage them to develop locomotor agility by following the parent in difficult movements. These selective advantages may contribute to retention of olfactory sense during the dependency period (see above).

Just as the young squirrel must learn what is "climbable," so it must learn what is "edible," and foraging during the dependency period may provide that experience. Besides the selection of food, other feeding behavior, such as the opening of nuts, improves during this time (Shorten, 1954).

SUMMARY

Preliminary observations made during the spring of 1958 and that of 1959 on young gray squirrels (*Sciurus carolinensis*) point out new facts concerning the post-nest life dependency period. While following (probably the mother), young squirrels constantly nuzzle the adult's flanks, and probably are dependent upon both visual and olfactory stimuli to motivate the "following response." Selective advantages of retaining the olfactory sense as primary during this period are discussed, and the possibility of a rapid, emphatic learning of visual species recognition characters during the following response is suggested. The motor patterns of locomotion are well-developed and young probably

gain experience on how to use these while following. Foraging may also improve during the dependency period.

REFERENCES

BOWLBY, J. 1953. Critical phases in the development of social responses in man. *New Biol.*, **14**:25-32.

BRACKBILL, H. 1953. Cardinal's period of dependency. *Wilson Bull.*, **66**:153.

BURT, W. H. 1946. *Mammals of Michigan.* Univ. Mich. Press, Ann Arbor. 288 pp.

———1957. *Mammals of the Great Lakes Region. Ibid.* 246 pp.

FLYGER, V. A. 1951. A bibliography of the tree squirrels and other pertinent literature. *Penna. Cooper. Wildl. Research Unit Quart. Report*, **13**:19-38.

———1955. Implications of social behavior in Gray Squirrel management. *Trans. N. Amer. Wildl. Conf.*, **20**:281-289.

HAMILTON, W. J., JR. 1943. *The Mammals of Eastern United States.* Comstock, Ithaca. 432 pp.

McCLELLAND, E. 1948. Notes on the red squirrel in Pittsburgh. *Jour. Mamm.*, **29**:409-412.

NEAL, E. G. 1958. *The Badger.* Penguin Books, Harmondsworth, Middlesex. 158 pp.

SETON, E. T. 1928. *Lives of Game Animals.* Vol. IV. Doubleday, Doran, Garden City, N.Y. 949 pp.

SHORTEN, M. 1954. *Squirrels.* Collings, London. 212 pp.

SMITH, G. A. 1947. Baby squirrels have urge to climb. *Science News Letter*, **51**:326.

THORPE, W. H. 1956. *Learning and Instinct in Animals.* Harvard Univ. Press, Cambridge, Mass. 493 pp.

YOAKUM, C. S. 1902. Some experiments on the behavior of squirrels. *Jour. Comp. Neurology*, **19**:541-568.

On Another Biclitellate Earthworm[1]

G. E. GATES
University of Maine, Orono

The biclitellate condition has been recorded hitherto from five individuals (Gates, 1956b), including four *Lumbricus terrestris* L. and one *Eisenia foetida* (Savigny, 1826). The latter (Gates, 1956a, 1958) is relictus-like on one side of the body. The term "relictus-like" refers to the position of the reproductive apertures, well behind normal locations. Two specimens have been described in the literature on earthworms. The type of *relictus,* subsequently shown (Gates, 1956a) to be an aberrant specimen of *Lumbricus rubellus* Hoffmeister 1843, has male pores on segment xxviii. The relictus-like specimen from Arizona, originally referred to *Allolobophora caliginosa* (now known to be a complex of several morphologically distinguishable forms) but which can now be identified as *A. trapezoides* (Duges, 1828), has male pores on xxviii-xxix.

An additional biclitellate specimen of *E. foetida* that is relictus-like on both sides was found in a small sample (25 worms) from culture beds of an earthworm farm at Laconia, N. H. The aberrant worm became available through the courtesy of Mr. Oscar Morrisette.

Description

First functional dorsal pore at intersegmental furrow 5/6, a smaller pore-like marking at 4/5. Reproductive apertures at usual locations with reference to meridians of longitude such as B, mD, etc. Clitellum at maximal tumescence. Tubercula pubertatis unrecognizable. Calciferous gland extends, at least, through segments xviii-xxi. Gizzard in xxviii-xxix. Ventral blood vessel bifurcates in v, each branch passing anterolaterally beyond circumpharyngeal nerve commissures. Dorsal trunk unrecognizable anterior to 9/10 (invisible because of lack of blood?). Brain, anteriorly in iii. Balls of brown debris, such as may be found after breeding has ceased, are present in some seminal vesicles. Spermathecal ampullae are filled with a watery fluid.

Metamerism, along much of the main axis, is abnormal beginning with xiii which is involved in a spiral. Segment xix of left side ends mesially both dorsally and ventrally. Among abnormalities partly concealed by clitellar obliteration of intersegmental furrows are two compound metameres each of which seemingly is split into three segments on the opposite side. Helicometameres are frequent behind the clitellar region, the last terminating with the eighth segment from the hind end. Further specification as to the metameric anomalies is need-

[1] From research financed by the Rockefeller Foundation.

less, but their existence requires that the rest of the anatomy be characterized as to left or right sides of the body.

Left side. Segments, 164. Spermathecal pores at 15/16, 16/17, 17/18 and 20/21. Female pores, in xxi and xxv. Male tumescence, with normal cleft (male pore unrecognizable), in xxv. Clitellum on xlv-liii, lvii-lxi and lxv-lxvi.

Intestinal origin in region of xxv-xxvi. Typhlosole ends in 151st segment. Hearts in x-xviii and xxi. Testes and male funnels (unusually large), in xvi, xvii, xviii, xxi. Seminal vesicles, preseptal in xv, xvi and xvii, postseptal in xviii and xxii. Ovary, with mature ova (some in egg string) and female funnel in xx. Ovary (no egg string or mature ova) and normal female funnel in xxiv. Ovisac in xxi but none in xxv. Spermathecae in xv, xvi, xvii and xx. Male gonoducts, as on other side of body, could not be traced (ventral parietes extensively blistered).

Right side. Segments, 160. Spermathecal pores at 15/16, 16/17, 17/18. Female pores, in xxi and xxiii. Male tumescences, each with a cleft (but male pores unrecognizable), on xxv and xxvi. Clitellum on xliii-li and lv-lxiv.

Intestinal origin in xxvii. Typhlosole ends in 149th segment. Hearts in xi-xviii. Testes and unusually large male funnels in xvi, xvii, xviii. Male funnels of xvii and xviii, like those in xvii-xviii on left side, with brilliant spermatozoal iridescence. Other male funnels with no trace of the iridescence. Seminal vesicles, preseptal in xv and xvi, postseptal in xvii, xviii, xix. Ovary (no egg string or mature ova) and normal female funnel in xx. Ovary with mature ova (some in egg string) and female funnel in xxii. Ovisac present in xxiii but lacking in xxi. Spermathecae, preseptal as on left side, in xv, xvi, xvii.

DISCUSSION

Segment number in unamputated normal individuals of *E. foetida* in North America, according to the author's unpublished counts, is 90-120. There are, then, in the specimen now under consideration forty to seventy or even more extra metameres. They were not added on at the hind end of the body, the atyphlosolate portion of the intestine which extends through 11-13 segments (11-15 in normal specimens, Gates, unpublished manuscript) being of usual length. As the extra metameres were not produced in the normal annelid manner (by a growth zone in the anal region) they must have been inserted in some unusual way. Situation of the gonads (which have a uniform location in all normal earthworms) shows that some segments were inserted close to the front end, others further back and also differently on each side. Intercalations such as are presently required do not take place in any species of earthworm, so far as is known, after hatching. Their origin then must be sought during embryogenesis and presumbly after formation of the germ layer in which metameric segmentation first appears. Associated with that modification of mesoblast

development is an increase in number of fixed position organs such as testes and ovaries. Most of the divergence in location and number of those structures in previous specimens could be explained (Gates, 1956-1958) by halving of mesoblastic somites at appropriate levels provided each daughter portion retained full developmental capacity of the parent block. What then are the levels at which somite splitting, with retention of original potentiality, could provide the aberrations of the present specimen.

Hearts are present in normal individuals, according to previous records (Gates, 1956, p. 21) and subsequently secured data, only in vii-xi. Location of the first heart of the left side in x shows that three segments were intercalated anteriorly. The three somites that were halved are assumed, in absence of information permitting precise specification, to be those at the 4th to the 6th level, *i.e.,* those that otherwise would have become segments iv-vi. Presence of ten instead of five hearts requires each of the heart-producing somites at the 7th to the 11th levels to have been halved. The number of testes, seminal vesicles and spermathecae corroborates splitting of somites at the 10th and 11th levels. The two ovary-containing segments indicate that the somite at the 13th level also was halved. Since the male tumescences are in xxv instead of xv there must have been ten intercalations in front of the 15th level. Nine already have been accounted for. The other intercalation could have resulted from halving of a somite at the 12th or 14th level neither of which give rise to organs of fixed position. Location of the gizzard (normally in xvii) seems to require halving of a somite at the 15th or 16th level. The latter is the one involved as halving of the former would have given two segments with male tumescences as in the relictus-like worm from Arizona (Gates, 1956, p. 369).

The clitellum of normal American individuals of *E. foetida* that have been seen by the writer comprises 6-8 segments (see below). Clitellar extension through 16 segments of the present specimen suggests halving of eight somites which could have been at the 24th-31st, 25th-32d or 26th-33d levels. As the clitellum begins with the 45th segment, there are 21-11=10 or 20-11=9 yet to be accounted for if the first clitellar somite were originally at the 24th or 25th level. But splitting of each somite at the 17th-23d or 24th level will not provide the necessary intercalations. If the first clitellar somite were at the 26th level, only 19-11=8 insertions are required. Splitting of all but one of the somites at the 17th-25th levels permits the clitellum to begin with the 45th segment. The remainder of the 13-43 possible intercalations on the left side would then be between the 33d level and the last 13 segments. Absence of special organs obviates localization of insertions in that region. Unexplained by the somite halving is the separation of a normally continuous clitellum into three parts and more particularly presence of three non-clitellar somites between 29a and 29b (presumably) as well as between 31b and 32a.[2]

[2] Daughter somites are indicated by a and b after level of the parent block.

On the right side, location of the first heart shows four segments were intercalated anterior to vii. Though they could have arisen from splitting of somites at any four of the 2d[3] to the 6th levels, fragmentation is assumed to have been at the 3d to the 6th levels. Eight hearts require halving of only three of the somites at the 7th-11th levels. The testes show but one of the somites at the 10th-11th levels were halved, hence the others must have been two of those at the 7th-9th levels. Two ovary-containing segments require halving of the somite at the 13th level. Two male tumescences require halving of the somite at the 15th level. Location of the male tumescences in xxv-xxvi requires ten insertions in front of the 15th level. Only eight have been provided. The additional two intercalations must have been between the 11th and the 15th levels. Hence, somites at the 12th and 14th levels obviously were the ones involved. If the first clitellar somite was that at the 26th level as on the left side, any six of the ten somites at the 16th-25th levels could have been halved. Then, to produce the 19-segment clitellum of the right side, 9 of the somites at the 26th to the 35th level must have been halved while one was not. But the clitellum has not been found to extend, in normal specimens of *E. foetida,* into xxxv though limits often are difficult to determine precisely from external inspection. If the first clitellar somite of the right side was at the 25th level, 7 of the somites at the 16th-24th levels must have been halved. The 19-segment clitellum then would have been derived from splitting of all but one of the somites at the 25th to the 34th level. This appears to be less improbable as there is one record (Gates, 1943, p. 95) of a clitellum extending through xxxiv.[4] Somite halving on the right side does not explain separation of the clitellum by three non-clitellar segments into two discrete portions nor the presence of an agonadal metamere between the two that contain ovaries.

Inasmuch as development is determinate and gonads are organs of fixed position, the aberrant locations of testes and ovaries in the present specimen should have resulted not from organ shifts (*i.e.,* transfer of potentiality) but rather from somite translocations. The abnormality of so much of the external metamerism in the present specimen shows there had been, as it were, considerable interference to normal median union. Such "interference" must be common in lumbricid development judging from the anomalies of adult metamerism that are found so often. Those aberrations arise through union

[3] The most anterior split required in any of the author's specimens has been at the 2d level, *i.e.,* of the somite that becomes segment ii. The mesoderm of a more anterior portion of the embryo that becomes the peristomium (segment i) then may not be so organized as to be liable to fragmentation.

[4] The clitellum of *E. foetida,* according to Michaelsen (1900, p. 476 and repeated by Stephenson, 1923, p. 499, Cernosvitov & Evans, 1947, p. 22), covers 7-9 segments, 24, 25, 26-32. It covers, in North America according to the author's records, 6 segments (5 specimens), 7 segments (72 specimens), 8 segments (9 specimens), and is on 25, 26, 27-31, 32, 33, 34.

of a somite of one side with two or even three on the other side, union dorsally with one somite but ventrally with another somite of the opposite side, sometimes isolating a somite from any union.

The serial order of ovarian segments on the right side then could have resulted merely by a daughter half-somite from the 12th or from the 14th level being forced out of normal position and then in between 13a and 13b. On the left side more complicated rearrangements that seem to be required could have been made in several ways. Possibly daughter somite 11b was forced out of position, back of 12 and then into line again behind 13a while 13b was being pushed in between 14b and the undivided somite at the 15th level.

In the clitellar region, on each side of the body, somites presumably from the postclitellar region, were forced forward into positions so as to separate the clitellum into three and two portions, respectively, on left and right sides.

Halving of mesoblastic somites early in development of the aberrant worm explains adequately the number of segments and of fixed-position organs as well as much of the homoeosis. Situations of several organs that are not in normal serial order require *in toto* translocation of somites before and/or after halving. The mesoblast may then be divided during development into discrete somites that can be forced out of normal position and into quite unusual locations. If, however, the mesoblast is not physically separated into discrete units, it appears to be capable of being transected along potential somite boundaries. Fragments so produced can be rearranged without loss of developmental potentiality determined by the original axial positions.

Presence of an ovisac in a testis segment (as in Lxxi) raises no difficulties as its development there is believed to be induced by the ovary of 13a which became segment xx. Presence of a spermatheca in an ovarian segment (Lxx) also raises no questions even though the receptacles always are one or more segments in front of the female gonads in normal individuals. Development of the spermatheca obviously was controlled by the testis somite that became Lxxi. Presence of seminal vesicles in segments where they normally would not develop is due to induction from the male gonads.

Unilateral translocations of somites only are suggested above. If, however, somites can be forced from one side of the embryo to the other, various displacements of that sort could have produced the conditions exemplified by the present worm. Abortion and trisection (*cf.* compound metameres mentioned on p. 418) of somites were mentioned in previous communications as ways of providing unexplained residues of homoeosis in some of the previous specimens. Somite translocation was considered at the time but was not mentioned because of lack of evidence from fixed-position organs such as testes and ovaries. That evidence now has been found and in further aberrant specimens indications of translocation from one side to the other are awaited.

SUMMARY

Number of segments and of fixed-position organs in a biclitellate and relictus-like specimen of *E. foetida* are explained by somite halving, providing developmental potentiality of the parent block is retained. Out-of-order location of certain organs requires translocation into abnormal positions of embryonic somites. The translocations indicate that somites are discrete or that a continuous mesoblast can be transected at potential boundaries of the somites. Mesoblast in that portion of the embryo that becomes the first segment (peristomium and prostomium) does not appear to split. Halving is possible from level of the somite that becomes segment ii well back towards the hind end.

REFERENCES

CERNOSVITOV, L. AND A. C. EVANS 1947. Linnean Soc. London *Synopses of British Fauna.* 6. Lumbricidae. Pp. 30.

GATES, G. E. 1943. On some American and Oriental earthworms. *Ohio Jour. Sci.,* **43**:87-116.

———1956a. On another lumbricid earthworm with "relictus" characteristics and the disposition of Southern's species. *Ann. Mag. Nat. Hist.,* **9**(12): 369-373.

———1956b. Notes on American earthworms of the family Lumbricidae. III-VII. *Bull. Mus. Comp.* Zool., Harvard College, **115**:1-46.

———1956c. On the origin of the biclitellate condition in lumbricid earthworms. *Ann. Mag. Nat. Hist.,* **9**(12):577-581.

———1957. On the origin of the homoeosis in an abberrant earthworm of the lumbricid species *Allolobophora tuberculata* Eisen 1874. *Ibid.,* **10**(12): 204-208.

———1958. On homoeosis, as well as other abberrations, and their origin in an earthworm species *Eisenia foetida* (Savigny, 1826), along with some deductions as to morphogenesis in the Lumbricidae. *Am. Midland Nat.,* **59**:452-464.

MICHAELSEN, W. 1900. *Oligochaeta. Das Tierreich,* 10. Pp. xxix, 575. Berlin.

STEPHENSON, J. 1923. *Oligochaeta. The fauna of British India, including Ceylon and Burma.* London. Pp. xxiv, 518.

Biology of the Brook Stickleback Eucalia inconstans (Kirtland)

HOWARD E. WINN
University of Maryland, College Park

In recent years the sticklebacks, especially *Gasterosteus aculeatus*, have been utilized as a tool for behavioral studies by the ethologists of Europe. Very little is known about the reproduction of the brook stickleback (*Eucalia inconstans*) and such information would be useful for a comparison with the behavior and ecology of other sticklebacks. The purpose of the present paper is to present field and laboratory observations that were made on this species in Michigan from 1952 to 1954 and to summarize the literature known to the author.

A few authors have reported that this species builds a nest and has habits similar to other sticklebacks (Bean 1903; Barker, 1918; Evermann and Clark, 1920; Adams and Hankinson, 1928; and others). Barker (1918) and Jacobs (1948), however, are the only authors that have published more than a note on field observations of the breeding habits of *Eucalia*. The present paper verifies and expands considerably the available information. As nearly as possible each subject will be taken up in the natural sequence of events of the stickleback. In only the detailed laboratory data will the new information be segregated from the known information on this fish.

Acknowledgments.—I wish to express my appreciation to John Twente, Janet Twente, Quentin Pickering and Carolyn Winn for their aid in collecting. I am indebted to Dr. James Haley and Carolyn Winn who criticized the manuscript. Dr. James Haley kindly supplied the literature on the parasites found in this fish.

Localities and Methods

During 1952, 1953, and 1954 field observations were made in Sylvan Ponds in the Waterloo Recreation Area, T2S, R3E, S.6, Washtenaw Co., Michigan. These are small, spring-fed, impounded ponds used at times to hold trout and other game species. There was a thick growth of *Chara* sp. and algae in the ponds along with sticks, leaves, and other organic debris, and the bottom was silt and gravel. A few observations were made in a small spring-fed creek, on Packard Road between Ypsilanti and Ann Arbor, 1.5 miles east of U.S. Route 23, where the creek flowed through the Country Club Golf Course, R7E, T3S, S.6-7, Washtenaw Co., Michigan. It contained leaves, sticks, higher aquatic plants, and algae over a bottom that was heavily silted in most places.

Individuals from Sylvan ponds and the creek were placed in several tanks in the laboratory. The activities in one particular tank, Tank A, were observed in some detail. The tank was 45 x 25

x 30 cm high, and set in a shallow tap water bath. *Vallisneria* sp. was placed in one corner; *Chara* sp. was placed in another corner; and various sticks, pieces of leaves, and algae were added on top of the gravel bottom. On May 12, 1953 at 9:00 P.M., two ripe male and two ripe female sticklebacks were placed in the tank. The history of these individuals will be followed in some detail because reproduction was completed and could be carefully observed. The laboratory notes have been abbreviated and rephrased.

In order to induce the brook stickleback to breed in the laboratory the temperature was maintained several degrees below room temperature. Other items such as adequate space, nest materials and a nest site were properly supplied. In Tank A the temperatures were between 16 and 17°C except for the first day (19°C) and the last one or two days (18°C). In a second tank where limited spawning success was obtained the temperature varied from 17 to 18.5°C. Other sticklebacks kept at temperatures ranging from 19.5 to 24°C did not breed. In one instance a nest was started but never completed and in another, eggs were laid in a completed nest, but they were destroyed by the sticklebacks themselves before the reproductive cycle was completed. In the other aquaria at these higher temperatures there was no sign of nest building or sequential breeding behavior. Adams and Hankinson (1928) reported that several authors were not able to spawn this species in aquaria. It appears as though this is not true if the temperatures are kept at least several degrees below 20°C.

HABITAT

Various authors have reported the habitat of *E. inconstans* to be small streams, ponds, alkali lakes, spring holes, and swampy margins and beach ponds of larger lakes (Bajkov, 1930; Barker, 1918; Cox, 1922; Evermann and Clark, 1920; Hankinson, 1916; Hubbs and Lagler, 1947; and Miller, 1957). These fish live in waters characterized as cold, clear, and heavily vegetated. The small stream, Sylvan Ponds, and several places along the shore of Lake Michigan where sticklebacks have been noted were all spring-fed. Miller (1957) reported this stickleback to be common in the potholes of Alberta which are spring-fed lakes. Other localities in southern Michigan known to the author where the brook stickleback was common also were spring-fed. Trautman (1957) reported the occurrence of this species as common in spring-fed areas of northeast Ohio. This represents its southern limit at that point. The most notable factor correlated with springs is a low temperature. It appears that temperature limits the southern distribution and habitat of *E. inconstans*. The few isolated populations of northern Ohio and southern Michigan may represent remnants of more widespread populations present during the Pleistocene. Unless it becomes climatically colder in these areas one can visualize the southern boundary of the range as slowly moving northward due to man's activities and climatic warming.

Age, Food, Parasites, and Predators

Jacobs (1948) stated that sexual maturity was attained in one year. An impression of the size categories in Sylvan Ponds suggests that the population was made up mostly of one-year-old, some two-year-old, and possibly a few three-year-old fish. The ponds were poisoned with rotenone in the fall of 1952. A small population was still present the next spawning season. However, the next or second spawning season after poisoning the population attained its original density. This fact supports the idea that sexual maturity is attained in one year.

A large number of notes have been recorded on food items (Adams and Hankinson, 1928; Clemens, *et al.*, 1924; Evermann and Clark, 1920; Forbes, 1883; Greeley, 1927; Hankinson, 1916; Pearse, 1918; Pettit, 1902; Toner, 1933; and Woolman, 1895). It is concluded from these reports that this fish is carnivorous. A wide variety of aquatic insects (especially larvae) and crustaceans are the principle food items. Other items mentioned are as follows: snails, water mites, algae, fish eggs (their own and others), and oligochaetes. Although a considerable number of statements have been made about the brook stickleback eating fish eggs, the actual data demonstrate that these are a minor dietary item.

Various studies have pointed out that the stickleback is preyed upon by some fish and birds but usually is only a minor food item. Various predators are as follows: bowfin (Lagler and Hubbs, 1940), yellow perch, largemoth bass (Evermann and Clark, 1920), northern pike (Hunt and Carbine, 1951), pikeperch (Maloney and Johnson, 1957), brook trout (Ricker, 1930), belted kingfisher (Salyer and Lagler, 1949), laughing gulls and common terns (Pope, 1909).

The following parasites have been recorded for *E. inconstans:* TREMATODA — *Bunoderina eucaliae, Crepotrema funduli, Neascus* sp., *Tetracotyle* sp., *Gyrodactylus eucaliae; Diplostomum baeri eucaliae;* CESTODA — *Proteocephalus* sp.; NEMATODA — *Agamonema* sp., *Contracaecum* sp., *Rhabdochona cascadilla, Spinitectus gracilis, Spiroxys* sp.; ACANTHOCEPHALA — *Neoechinorhynchus rutili, Neoechinorhynchus* sp., *Leptorhynchoides thecatus* and *Pomphorhynchus bulbocolli* (Bangham, 1937; Bangham and Hunter, 1939; Fischthal, 1947, 1950, 1952; Hoffman and Hundley, 1957; Hoffman and Hoyme, 1958; Ikezaki and Hoffman, 1957).

Migration and Reproductive Period

Characteristically the brook stickleback migrates into shallow water to spawn in the spring, after which it gradually moves to deeper water or downstream in the summer. Applegate and Brynildson (1952) recorded a downstream movement during the fall and winter in northern Michigan, and Evermann and Clark (1920) said they were found in deeper water among vegetation in the summer, and in shallower water in winter and early spring. There is only a minimum of information on these movements.

Eucalia spawns in southern Michigan from late April or early May to the middle of June, but in northern Michigan they complete spawning about one month later. Nests with eggs were at least present in May and early June in Sylvan Ponds. Although over 25 nests were seen June 5 and 6, only 8 could be located on June 15, 1952, at which time all the eggs were well developed. In the same ponds during 1953 nests with non-eyed eggs were located on May 17 and nests were still present on the first of June. A few nests, with and without eggs, were found May 9, 1954. In the creek, nests were not found (May 12 and 16) until May 18, 1953 and none were found after June 15. Nests were seen in northern Michigan in early July near the Michigan Biological Station, Emmet Co. and by the shore of Lake Michigan near Cross Village, Emmet Co., on July 6, 1952. Temperatures recorded when nests were found were normally 15 to 19°C. In several situations just at the end of the nesting season temperatures rose to 27°C. Successful reproduction in aquaria occurred at 16 to 18°C. Barker (1918) stated that in central New York nesting begins at 40 - 50°F (5 - 10°C) and ends at 70°F (21°C) during April and May. According to Jacobs (1948) nesting begins in late March or early April and continues until June in the southern half of Minnesota. He further stated that the water must attain a minimum of 8°C before spawning begins. Harkness and Ricker (1929) found nests and eggs on July 1 in Ontario, Canada. From the above data it appears that spawning occurs later in more northerly latitudes as is generally true for many of our northern temperate freshwater fishes.

COURTSHIP, SPAWNING AND CARE OF EGGS

These subjects are divided into two main sections. One section describing observations in the laboratory presents a complete sequence of reproductive events in a situation where close accurate observations could be made. A second section relates our observations to those of other workers, discusses, and summarizes the activities.

OBSERVATIONS ON TANK A

The conditions of this tank are given under localities and methods.

May 12, 1953, 9:00 P.M.—Two ripe males and females placed in tank. Males were a light color like the females.

May 13, 9:00 A.M.—One male was almost jet black. This one is referred to as R male because he built a nest in the right side of the tank. The other is L male, in the left side of tank.

10:30 A.M.—Both males were almost jet black. One female was light colored and the other was black and gray-green variegated. Male R chased the light female who went to the bottom. The variegated female was near the surface. When the tank was disturbed, male R lightened in color but immediately darkened when he had a brief fight with the other male.

12:30 P.M.—Male R picked up a small piece of plant and carried it for a few seconds.

1:15 P.M.—Several sticks were added to the tank.

2:00 P.M.—The first piece of plant was attached to a stick within the next half hour.

4:15 P.M.—Male R had a few pieces of root and alga attached to a stick on the right side of the tank.

9:00 P.M.—Male R now had attached enough material to the crotch of a branch so that the outline of a nest was discernible. The males chased the females when they came near. Male R with a nest defended the right side of the tank and male L without a nest defended the left side of the tank. Male R chased a female into male L's territory twice. This carried male R into male L's territory from which male R was chased. Several times male R chased other fish. Male R attacked a finger placed near the nest. Active movement by the observer resulted in the male becoming temporarily lighter. Male R mouthed several pieces of alga before he placed them individually onto the nest. Then the male encircled the nest in many directions poking his snout at it and slightly pushing at material attached to the nest. Thus far mostly alga with only a few small pieces of roots had been used. He picked up a long strand of alga and moved his mouth over it and then spit it out. This action was repeated many times with some material put in the nest and some pieces rejected.

9:30 P.M.—Lights turned out. After one hour a light was turned on. The male was beside the nest and in a few seconds began to move rapidly.

May 14, 6:45 A.M.—The nest was completely formed but the male still added material to it. He may have worked at night. Male L has not attempted to start a nest. Another stick was added to L's territory. The nest (R) has only one hole and the male put his head in it several times. This pushing of the head kept an open space inside the nest and maintained the circular form of the hole. The male picked up many pieces of material some of which was rejected and some of which was added to the nest. Between these acts he curved his body to the contours of the nest and moved over its surface. Frequently he circled the nest "as though looking at it." The abdomen of one female was no longer enlarged. She may have released her eggs outside the nest. She was removed. Male R entered male L's territory and promptly was chased out.

1:00 P.M.—Another observer noted nest-building activities similar to those described above. One piece of plant was brought out from inside the nest, held in the male's mouth, and then was spit out.

9:30 P.M.—Nest-building activities and territorial chases were observed.

May 15, 9:00 A.M.—The remaining female was removed because she was thin and had apparently released her eggs outside of the nest. She was no longer variegated. The male added no material to the nest but spent most of his time poking his head inside the nest hole.

May 16, 2:30 P.M.—Two ripe females were added (2 females and 2 males now present). One went near male R and he attacked her vigorously. He hit her body with his snout several times until she left. Then he went to the nest and touched his mouth around the rim of the nest. Male L hit each female

as she entered his territory. Soon the females were chased from territory to territory. Male R swam into male L's territory and was chased, but as soon as he re-entered his own territory he stopped and turned. Male L did not enter male R's territory. The two males fought briefly at the boundary area. It appeared as though the R male placed some white fluid over the rim of the nest. This was done by touching the nest with the urogenital area. This was presumed to be the kidney secretory material used in binding the nest materials together. The male now spent considerable time mouthing the nest whereas the females, which had changed from a dark variegated appearance to a relatively uniform coloration, were hidden under the alga and in plants. The male R bit at several pieces of alga.

May 17, morning—Male R chased the now variegated females several times. There were eggs in the nest now, but a second hole, which would have been produced by the female as she swam through the nest, was not present. The male must have patched up the second hole. Male R stuck his head in the hole, pulled his head out, and wiggled in front of nest opening, moving the pectoral fins back and forth. This caused an observable current of water to pass over the eggs. The male fanned the nest briefly several times. In between times the male went around the nest poking his head at it. Two ripe females were added to the tank (4 females now in tank, one spent).

7:00 P.M.—Male R frequently chased ripe females, the spent female, and male L and in between he fanned eggs. Male L also chased females. Occasionally both males nipped at the females. Once, male L grabbed the pectoral fin of a female. The males acted as though an invisible line or very narrow space divided their territories. Once over this boundary a chased male stopped fleeing. He would turn and attack if the other male crossed over. Male R seemed much more vigorous in his attacks. In abbreviated form, what follows is a description of fifteen minutes activity by male R minute by minute: minute (1) head in nest, fanned eggs, chased females, fanned, chased female; (2) fanned, chased female; (3) head in nest, fanned; (4) head in nest, fanned; (5) repaired nest; (6) repaired nest, chased female; (7) head in nest, fanned; (8) fanned, chased female, chased female; (9) head in nest, fanned; (10) head in nest, fanned, chased female; (11) head in nest, fanned, chased female; (12) fanned, head in nest, fanned; (13) repaired nest; (14) head in nest, fanned, chased female; (15) chased female, fanned, chased female. This demonstrates the rapidity of activities by the nest-guarding male. The fanning of the eggs lasted from 1 to 3 seconds.

May 18, 8:30 A.M.—Male R vigorously chased females, poked head in nest, fanned eggs, and "inspected" nest several times within a few minutes. More eggs were in nest. Small pieces of a white substance were evident on nest and on bottom of tank.

1:00 P.M.—One gravid female was added to the nest (5 females in tank). Male R reacted as follows: went to her and bit her tail; bit again and she went to bottom; male placed head in nest and fanned eggs; went to female; bit and chased her actively; fanned eggs; and chased her again.

7:00 P.M.—Three partially spent females were removed and one ripe female added. This left three ripe females in the tank. Male R attacked and bit the net and a finger placed in the tank.

9:00 P.M.—One female was in the nest with her head sticking out of the nest opposite the regular opening. Observer chased her out. She came back to

nest area and male R attacked her once. She did not flee. The male went then to the entrance of nest. She followed and entered nest. Observer chased her out again. The male then moved eggs in the nest and fanned them. It appeared as though this kept an empty space in the nest as eggs were pushed to the side and down. The female came near the nest again. The male immediately went to the entrance of the nest and back to her. Observer chased her away. The male attacked her, she did not move and he then went to nest entrance. She entered nest. The male nudged his snout against the female's caudal peduncle. After 7 nudges the female vibrated vigorously; 2 nudges by male and the female vibrated again; and she vibrated again after three nudges. The female after 4 minutes then swam out the back side of the nest. The male immediately swam through the nest after her with only a brief pause over the eggs. It is presumed that the eggs were fertilized when the male went rapidly through the nest. The male then chased the less plump female out of his territory. He put his head in the nest and arranged the eggs by pushing them to the side and bottom. Male L was not as dark as male R.

May 19, 7:30 A.M.—Nest repair, egg-fanning, and territorial defense activities were observed.

May 20, 3:30 P.M.—A female was in the nest and the male poked at her caudal peduncle. During the fifteen-minute period in the nest she vibrated vigorously sixteen times. When she left the nest the male passed through the nest vibrating vigorously with only a seconds' pause inside the nest.

May 21—Nest R was much larger than when first completed, and, in fact, much larger than any comparable nest found in the field. Egg-fanning was observed.

May 22, 7:40 A.M.—The male added some material to the nest and the usual activities were observed.

May 24, 8:30 P.M.—Male L had built half of a nest. Two ripe females were added. The new nest was tied to two sticks, a *Vallisneria* frond and a bladderwort branch. It consisted of a few roots, a few bits of plants and mostly algal pieces. Male R still added material to his nest. An algal covering can be seen over the eggs inside the entrance. Male R performed his usual activities. The largest female nipped at the other females. A ripe female was now in the black variegated color pattern.

May 25, 11:15 A.M.—Male L now had a larger nest with eggs in it and he was fanning at the nest entrance for the first time.

May 26, morning.—The first young were observed at male R's nest around the entrance and on the surface of the nest. The male was fanning eggs at intervals of 4 to 6 seconds, which was an increase over the periods of 1 to 3 seconds first observed. There was also an increase in the frequency of fanning. The male dashed from place to place around the nest and poked rapidly at various parts of nest but did not add any material to it. The number of times a male fanned eggs was counted for 6 periods of five minutes each with the following results: male R, 8, 8, 9, 10, 9, and 10; and male L, 1, 3, 1, 2, 2, and 2. Almost every time male L fanned his eggs he also poked his head into the nest which resulted in the eggs being pushed to the side of nest. Male R with young did this about once out of every three times that he fanned the eggs. Eight larval fish (*Etheostoma nigrum*) introduced near male R were not eaten, whereas of ten larvae dropped near two males guard-

ing only eggs six were eaten. ***Daphnia*** and white worms were eaten by all males.

May 26, 7:00 P.M.—Movements of the young were observed. One went to the surface of the water and dropped back down on the outside of the nest near another larva. Male R came up, drew both young into his mouth, put his head into the nest and spit them out. He picked up two more young and spit them into the nest, which by now was somewhat deteriorated. He did the same with another larva and then pushed a piece of material against the nest. One larva swam to the surface and the male took him in his mouth. A female approached and the male postured at her by placing head downward and erecting the pelvic spine on her side. Then he spit the larva into the nest. At this point a series of experiments were carried out where individual larvae of *Etheostoma nigrum* were dropped near the L and R male sticklebacks. The results are given in Table I and will be discussed in the next section. The male had been actively grabbing his larvae and spitting them into the nest. The male took one dead larva out of nest and spit it out.

8:30 P.M.—The male has fanned the eggs and spit many young into the nest, but the young swam from the nest almost as fast as the male could retrieve them.

9:30 P.M.—The lights were turned out for five minutes. When the light was turned on, the young were seen scattered all over the tank and three females were near male R's nest. He immediately chased them away.

May 27, morning.—Male R spit many young into the nest. One female in the black variegated color pattern tried to get into R's nest. Many more young were outside of the nest than previously.

5:00 P.M.—An aggregation of young formed in the water above the nest. Many young were still on and in the nest.

7:00 P.M.—All or most of the young had been put back in the nest. When a flashlight was turned on a few larvae became active, but they were grabbed immediately by male R and spit into the nest. He repeated this action well over 100 times between 7:00 P.M. and 8:30 P.M.

May 28, 8:30 A.M.—A large aggregation of larvae were seen above the nest and many were seen on and in the nest. The male occasionally picked up one and spit it into the nest, but when he did this 2 to 5 other young came out of the nest. The male defended his territory actively any time it was entered by a female or by male L. Several times he chased a female when he had young in his mouth, but he did not bite her and immediately afterwards went to the nest and spit the young into it. The male usually picked up one larva and then spit it into the nest but several times two larvae were picked up and spit into the nest.

4:00 P.M.—The male occasionally spit larvae, one, two or three at a time into the side of the nest which by now consisted of just a mass of disorganized alga, but most of his time was now spent in territorial defense.

6:30 P.M.—Many larvae were in, on, and above the algal mass. The male continued to pick them up and spit them into the nest. The numbers picked up and spit into nest were as follows: 20 times one larvae picked up; 5 times two; and once three and once four. There were no eggs in the nest. Occasionally he stopped to attack an intruder. He returned 38 young to the nest

in 15 minutes (27 retrieving acts). It was almost dark. The first young were taken from the outskirts of the territory. When they were in the nest he started retrieving those in an aggregation above the nest. The young did not come out of the alga as they had during the day.

9:00 P.M.—Most of the young were in the algal remains of the nest.

May 29, morning.—The nest was no longer recognizable. The male circled the young occasionally and picked up a few and spit them into algae near where the nest was once located.

May 30.—Many young were scattered all over the tank.

June 1.—Males still maintained territories. Many young have disappeared.

June 3, 7:00 P.M.—First young seen in male L's nest.

June 4, 12:00 Noon.—Many young were around L nest.

7:30 P.M.—The nest was already slightly deteriorated and the male spit many young into the nest.

June 6, 1:00 P.M.—Male L was dying. Young have scattered throughout the tank. A few of male R's young were still present and male R still maintained a territory. (End of observations.)

SUMMARY AND COMPARISON OF OBSERVATIONS

Barker (1918) and Jacobs (1948) have given the following information on the breeding of the brook stickleback based on field observations: males were jet black during the spawning season; the male defended the nest which he built until the young hatched; the male fanned the eggs; female and male in an excited dance circled and butted until she entered the nest; then the male entered the nest to fertilize the eggs; male secreted material from the kidneys to glue the nest; and two or more females spawned in the same nest, laying up to 250 eggs or more each. The present observations expand upon the above and are essentially in agreement with them except on two points. It should be mentioned that it is assumed that the eggs were fertilized when the male passed through the nest. Also, it was assumed that the kidney secreted the material to glue the nest, although Jacobs *op. cit.* stated testes instead. The two points of disagreement are that the sticklebacks also guard the young after hatching (not just to hatching) and the description of an excited courtship dance by Jacobs *op. cit.* was not verified.

Almost all the activities observed in Tank A were also observed in the field with a greatly reduced frequency and in another aquarium.

First the males arrive in shallow water in the spring where they establish territories and start to build nests. Jacobs (1948) noted that a male may build two successful nests in one season. In the present observations some males were jet black before the nest was started and others became so only after the nest was completed.

The territories are defended against individuals of a reasonable

size of most species. Darters were attacked in aquaria and in the field. *Gambusia affinis* and a trout were chased. This defense was maintained both in the field and laboratory until after the young left what remained of the nest. Rather narrow boundaries existed between territories which the males were able to recognize. A male chasing another male often crossed his boundary and thus in turn was chased. If a male was in one side of his territory, an intruder male on the opposite side frequently penetrated more deeply into the territory before he was chased. Ritualized fights between males with spines erect were observed in the laboratory but infrequently in the field. One other fact was noted about the mapped territories in Sylvan Ponds. The ponds were poisoned between the 1952 and 1953 spawning season. The individual males of the much smaller 1953 population maintained larger territories. Furthermore, many males nested in the upper, middle and lower Sylvan Ponds in 1952. Only three or four nests were found in the upper pond, none in the middle and a fair number in the lower pond in 1953. All ponds had many males with nests in 1954. Only one year was required for the sticklebacks to attain their original population size.

In Sylvan Ponds while the males maintained territories and built nests the females swam in aggregations or individually outside of the males' area. Female dominance, noted in aquaria several times, was never observed in the field. When a female was ready to spawn her color changed from a uniform pale green to a variegated dark and light pattern. She then entered the male's territory where she was attacked. She responded in one of four ways to the male nips and butts. She moved toward the nest, remained motionless, went to the bottom, or moved on to another territory. If she remained still or went to the bottom, the male frequently would go to the opening of the nest. If she did not come to the nest, he would go back to her and the process was repeated. Several times nudges by the male appeared to direct the female towards the nest. Eventually the female entered a nest. In this position, with her head and tail sticking out each side of the nest, the male prodded her ventral region and her caudal peduncle. This resulted in her vibrating vigorously at which time presumably she laid eggs. After the female had vibrated, usually several to many times, she swam out of the nest where she was attacked frequently by the male. This does not seem to fit precisely Jacobs' (1948) brief descriptions of an excited courtship dance. She fled immediately to an area outside of the males' territories. Several times females attempted to enter nests too small for them so that the nests were partially destroyed. This fact would certainly select against individuals who had the tendency to build a nest too small.

The male cared for the nest by the continued addition of material and the repair of loose material. After eggs were laid in the nest, the male pushed them to the side and down. This left a space (through the center of the nest) across the nest and opposite the entrance. Barker (1918) reported that a male spit loose eggs at the entrance

into the nest. A male spent a great deal of time fanning his pectorals at the entrance of a nest with eggs. This activity increased in length of time and frequency as the eggs developed. A male with eggs was mainly occupied with repair of nest, arrangement of eggs, territorial defense and fanning of eggs. These were less frequent in the field than they were in Tank A (see May 17) probably because of the usually greater distances traveled in defense of a territory.

Finally after the eggs hatched, the male retained a territory around the tattered remains of the nest which swarmed with the larvae. This was apparently ended when the larvae swam fast and continuously enough so that the male was unable to retrieve them efficiently. For the first three or more days, the larvae spent a great deal of time in one position with their heads against the nest or other objects but at various angles to them. Larvae of *Etheostoma nigrum* were introduced to a male with only eggs and a male with eggs and young (Table I). The male with only eggs ate most of the dead and live larvae. The male with eggs and young retrieved most of the live ones and spit them into the nest whereas most of the dead ones were apparently disregarded. There is a distinct difference in approach between the two males and the underlying mechanism that causes the change needs to be investigated. The male with young could usually discriminate visually between a dead and live larva, yet he ate white worms and *Daphnia* at this time.

NESTS, EGGS, AND YOUNG

In general, the nests were roughly globular in shape and constructed variously of organic debris, algae and other materials. The nests were usually attached to a stem, on the bottom to over one foot

TABLE I.—Responses of male brook sticklebacks in Tank A on May 26 to larvae of *Etheostoma nigrum* when they were placed individually in the aquarium.

	No. Eaten	No. Disregarded	No. Inspected	No. Taken in Mouth and Spit out	No. Taken in Mouth and Spit in Nest
	Dead Larvae				
Male with young and eggs (Male R)	0	11	3	3	0
Male with only eggs (Male L)	13	1	0	1	0
	Live Larvae				
Male with young and eggs (Male R)	0	1	3	2	10
Male with only eggs (Male L)	5	0	0	0	0

above it. Barker (1918) reported finding nests of three quarters of an inch in diameter and fastened to a rootlet or grass blade. Jacobs (1948) said that the nests averaged 30 mm in diameter and were attached under cover to twigs or plant stems just above the bottom. The present observations expand upon these notes. The nests need not be under cover and diameters varied from 1.5 cm to 5 cm. They increased in size over the season as eggs were added and as the male added material to the nest. The bottom varied from organic debris to sand and various mixtures of both. In two years of observation at Sylvan Ponds, four nests were in contact with the bottom and forty were off the bottom although they were most commonly just off the bottom. Also, eight nests were found attached to the horizontal branch of a dead stem; four to logs, six to a vertical branch, 28 to vertical branches of live *Chara;* three to leaves; one to another vertical plant stalk; and 15 to dead horizontal stalks of plant stems. Some nests observed in Lake Michigan were attached to *Scirpus* stalks and to blades of grass bound together. Many more nests (80%) were found on *Chara* stalks in 1954 than in 1953 (5%). It could mean that sticks are preferred and the *Chara* is a second choice. The lowered population in 1953 resulted in mostly the use of sticks whereas many individuals of a greatly increased population in 1954 had to resort to the use of *Chara.* This will also vary according to the materials available and probably these variations can be greatly expanded when many populations over wide areas are investigated.

Barker (1918) said the nests were constructed of dead grass blades, fibers, etc., and later in the season, algae and seed sprouts. Jacobs (1948) reported nests made of plant pieces. Almost any sort of light small pieces of plant debris are used. Some of them found in this study were as follows: small sticks, pieces of many kinds of plants, *Chara,* duckweed and algae (very common).

Barker (1918) reported that in his study each nest had a single opening, while Jacobs (1948) stated that each nest had two openings. In the present study nests both with one and with two holes were found depending upon the occurrence of specific events. All the nests had one opening prior to the deposition of eggs by a female. She created a second hole upon leaving the nest through the side opposite the entrance maintained by the male. This second hole was repaired with varying degrees of success by the male, but such repair was observed much less often near the end of the spawning season. One nest was found with three holes in it, two of which were probably created by two different females.

Barker (1918) described the eggs as transparent and light yellow with a diameter of about 1 mm. He reported that the larvae hatched in eight or nine days at 20.5°C., were 5 mm in length at hatching and then attached by their head to various materials for the first few days. Jacobs (1948) reported that the eggs were 1.3 mm in diameter, colorless, and the young attached by the tip of the head possibly by means of a viscid spot. The eggs seen in this study were

as Barker described them and were also demersal and adhesive. The two sets of eggs observed in this study hatched as follows: 203 to 232 hours at 16° to 17°C and 220 to 259 hours at 17° to 18°C. The yolk sac was absorbed in about 100 hours. As for the young hanging by their head from objects, this could be explained by movements of the pectoral and caudal fins rather than by any viscid spot. The large number of observations made on this point will not be described because a definitive interpretation could not be made.

SUMMARY

The biology of the brook stickleback with emphasis on reproduction is described with the inclusion of all the literature available to the author at this time.

The brook stickleback lives in small pond-like areas and streams where the water is clear and where heavy vegetation occurs. It is restricted essentially to spring-fed areas in Ohio and southern Michigan.

The fish mature in one year, eat primarily insects and crustaceans and are eaten occasionally by some fish which are listed.

The fish migrate to shallow water to spawn in April, May and June at temperatures between at least 15° and 19°C. The nesting period starts later in the season north of southern Michigan.

A detailed description is given of their reproductive activities under laboratory conditions. This is then broadened to include field observations and those of other authors. The following activities are described: territoriality, nest building and repair, spawning, egg fanning, caring for eggs, and caring for young. Males with only eggs ate young larvae placed near them, whereas, males with young retrieved the larvae if alive and spit them into the nest.

The nests may have one or two holes. The second is produced by the female and variously repaired by the male. The nests are made of bits of dead organic debris and various pieces of live plants such as algae. The positions of nests are given and they are most often placed just off the bottom attached to some object. The eggs are described and hatching times given.

REFERENCES

ADAMS, C. C. AND T. L. HANKINSON 1928. The ecology and economics of Oneida Lake fish. *Roosevelt Wild Life Ann.*, **1**:235-548.

APPLEGATE, V. C. AND C. L. BRYNILDSON 1952. Downstream movement of recently transformed sea lampreys, *Petromyzon marinus*, in the Carp Lake River, Michigan. *Trans. Amer. Fish. Soc.*, 1951, **81**:275-290.

BAJKOV, A. 1930. Fishing industry and fisheries investigations in the prairie provinces. *Ibid.*, **60**:215-237.

BANGHAM, R. V. 1937. Parasites of Wayne County (Ohio) stream fish. *Ibid.*, 1936, **66**:357-358.

——— AND G. W. HUNTER, III 1939. Studies on fish parasites of Lake Erie. Distribution studies. *Zoologica,* **24**:385-448.

BARKER, E. E. 1918. The brook stickleback. *Sci. Monthly,* **6**:526-529.

BEAN, T. H. 1903. Catalogue of the fishes of New York. *Bull. N. Y. St. Mus.,* **60**:1-784.

CLEMENS, W. A., J. R. DYMOND, AND N. K. BIGELOW 1924. Food studies of Lake Nipigon Fishes. Univ. of Toronto Studies, Biol. Series, No. 25, *Publ. Ontario Fish. Res. Lab.* No. **25**, pp. 103-165.

COX, P. 1922. Results of the Hudson Bay Expedition, 1920. II. The Gasterosteidae. *Contrib. Canadian Biol.,* 1921, pp. 151-153.

EVERMANN, B. W. AND H. W. CLARK 1920. Lake Maxinkuckee, a physical and biological survey. *Indiana Dept. of Conserv.,* **1**:1-660.

FISCHTHAL, J. H. 1947. Parasites of northwest Wisconsin fishes. I. The 1944 survey. *Trans. Wisc. Acad. Sciences, Arts and Letters,* 1945, **37**: 157-220.

———1950. Parasites of northwest Wisconsin fishes. II. The 1945 survey. *Ibid.,* **40**:87-113.

———1952. Parasites of northwest Wisconsin fishes. III. The 1946 survey. *Ibid.,* **41**:17-56.

FORBES, S. A. 1883. The food of the smaller freshwater fishes. *Bull. Ill. St. Lab. Nat. Hist.,* **1**:65-94.

GREELEY, J. R. 1927. Fishes of the Genesee River System. N. Y. St. Conserv. Dept., *Supp. to 16th Ann. Rept.,* 1926, pp. 47-66.

HANKINSON, T. L. 1916. Results of the Shiras Expeditions to Whitefish Point, Michigan: Fishes. *Mich. Geol. and Biol. Surv. Publ.,* **20**, Biol. Series 4, pp. 111-170.

HARKNESS, W. J. K. AND W. E. RICKER 1929. A preliminary study of some trout waters of Ontario. *Trans. Amer. Fish. Soc.,* **59**:256-267.

HOFFMAN, G. L. AND J. B. HOYME 1958. The experimental histopathology of the "tumor" on the brain of the stickleback caused by *Diplostomum baeri eucaliae,* Hoffman and Hundley, 1937 (Trematoda:Strigeoidea). *J. Parasitol.,* **44**:374-378.

——— AND J. B. HUNDLEY 1957. The life cycle of *Diplostomum baeri eucaliae* n. subsp. (Trematoda:Strigeida). *Ibid.,* **43**:613-627.

HUBBS, C. L. AND K. F. LAGLER 1947. Fishes of the Great Lakes region. *Cranbrook Institu. of Sci., Bull.* **26**, pp. 1-186.

HUNT, B. P. AND W. F. CARBINE 1951. Food of young pike, *Esox lucius* L., and associated fishes in Peterson's Ditches, Houghton Lake, Michigan. *Trans. Amer. Fish. Soc.,* 1950, **80**:67-83.

IKEZAKI, F. M. AND G. L. HOFFMAN 1957. *Gyrodactylus eucaliae* n. sp. (Trematoda:Mongenea) from the brook stickleback, *Eucalia inconstans. J. Parasitol.,* **43**:451-455.

JACOBS, D. L. 1948. Nesting of the brook stickleback. *Proc. Minn. Acad. Sci.,* (abstract) **16**:33-34.

LAGLER, K. L. AND F. V. HUBBS 1940. Food of the long-nosed gar (*Lepisosteus osseus oxyurus*) and the bowfin (*Amia calva*) in southern Michigan. *Copeia,* **1940**:239-241.

MALONEY, J. E. AND F. H. JOHNSON 1957. Life histories and inter-relationships of walleye and yellow perch, especially during their first summer in two Minnesota lakes. *Trans. Amer. Fish. Soc.,* 1955, **85**:191-202.

MILLER, R. B. 1957. Alberta's "Pothole" trout fisheries. *Ibid.,* 1956, **86**: 261-268.

PEARSE, A. S. 1918. The food of the shore fishes of certain Wisconsin lakes. *Bull. U. S. Bur. of Fish.*, **35**:249-292.

PETTIT, R. H. 1902. *Eucalia inconstans* destructive to mosquitoes. *Spec. Bull. Agric. Exp. Sta., Mich. Agric. College*, **17**:9.

POPE, T. E. B. 1909. Devil's Lake, North Dakota. A study of physical and biological conditions, with a view to the acclimatization of fish. *U. S. Bur. of Fish. Rept. for 1907*, pp. 1-22.

RICKER, W. E. 1930. Feeding habits of speckled trout in Ontario waters. *Trans. Amer. Fish. Soc.*, **60**:64-72.

SALYER, J. C. AND K. F. LAGLER 1949. The eastern belted kingfisher, *Megaceryle alcyon alcyon* (Linnaeus) in relation to fish management. *Ibid.*, (1946) **76**:97-120.

TRAUTMAN, M. B. 1957. *The Fishes of Ohio*. Ohio State Univ. Press, pp. 1-683.

TONER, G. C. 1933. Annotated list of fishes of Georgian Bay. *Copeia*, **1933**: 133-140.

WOOLMAN, A. J. 1895. A report upon ichthyological investigations in western Minnesota and eastern North Dakota. *U. S. Comm. of Fish and Fisheries Rept. for 1893*, **19**:343-373.

Studies on the Trematode Family Brachycoeliidae. IV. A Revision of the Genus Mesocoelium Odhner, 1911; and the Status of Pintnaria Poche, 1907[1]

THOMAS C. CHENG
Lafayette College, Easton, Pennsylvania

This paper is the last of four concerned with the taxonomy of the trematode family Brachycoeliidae. Earlier ones (Cheng, 1958, 1959, 1960) dealt with the systematics of the genera *Brachycoelium* (Dujardin, 1845) Stiles and Hassall, 1898; *Leptophallus* Lühe, 1909; *Cymatocarpus* Braun, 1901; *Glypthelmins* Stafford, 1905; *Margeana* Cort, 1919; and *Reynoldstrema* Cheng, 1959. Their subfamilies were redefined by Cheng and Provenza (1960). The genus *Mesocoelium* Odhner, 1911, is discussed herein, and the monotypic *Pintnaria* Poche, 1907, is considered a synonym.

The author is grateful to Dr. Horton H. Hobbs, Jr., Professor of Biology, University of Virginia, and Director of Mountain Lake Biological Station, for reviewing this manuscript and offering several constructive criticisms.

The Genus MESOCOELIUM Odhner, 1911

The genus *Mesocoelium* was originally assigned to the subfamily Brachycoeliinae Looss, 1899 by Odhner (1911). Dollfus (1929) erected the subfamily Mesocoeliinae with *Mesocoelium* as the type genus, and later (1933) erected Mesocoeliidae to include this subfamily. Dollfus' system has not been widely accepted. The author, however, is of the opinion that in recognizing the family Brachycoeliidae Johnston, 1912, (see Cheng, 1959 and Cheng, 1960) Mesocoeliinae is of some systematic value as a subordinate group (Cheng, and Provenza, 1960).

The affinities between *Brachycoelium* and *Mesocoelium* are expressed in the morphology of the excretory vesicle, the flame-cell pattern, the general body outline and size, the location and ratios of the suckers, the shapes and relative sizes of the gonads, the distribution of the vitellaria, the specific category of hosts (*i.e.,* amphibians and reptiles), and the parallel life history patterns. In the opinion of the author, the differences in the relationship of the testes to the ovary and the comparative lengths of the intestinal ceca, justify the assignment of the two genera to separate subfamilies, Brachycoeliinae

[1] This research was supported (in part) by Grant-2086 from the National Science Foundation. A contribution from the Department of Biology and Mountain Lake Biological Station, University of Virginia, and the Jenks Biological Laboratories, Department of Biology, Lafayette College.

and Mesocoeliinae, an arrangement that Yamaguti (1958) has accepted.

Of the 32 described species of *Mesocoelium,* one, *M. sokolowi* Skrjabin, 1916, has been transferred to the genus *Anchitrema* by Dollfus (1929), where, in the author's opinion, it properly belongs. There is disagreement as to how many of the remaining species are valid, because they show marked morphological resemblances and have received little attention in recent years. An attempt is made here to clarify the matter by utilizing certain diagnostic characteristics which seem sufficiently consistent to be reliable.

The shape of the excretory vesicle apparently is useful in distinguishing species but is not known for all the species. Furthermore, in several instances the vesicle is Y-shaped but with extremely short cornua, making it debatable as to whether it is actually I- or Y-shaped. The author, therefore, has chosen not to rely heavily upon the shape of the excretory vesicle in separating species.

In the genus *Mesocoelium,* 3 distinct groups of species can be distinguished by the location of the testes. In the first group, which includes *M. sociale, M. microon, M. carli, M. meggitti, M. monodi, M. marrsi, M. danforthi, M. leiperi, M. crossophorum, M. schwetzi, M. maroccanum, M. lanceatum, M. elongatum, M. sibynomorphi, M. travassosi,* and *M. brachyenteron,* the testes are symmetrically placed on each side of the acetabulum; in the second group, including *M. ovatum, M. japonicum, M. americanum,* and *M. minutum,* the testes are anterior to the level of the acetabulum; and in the third group, including *M. incognitum, M. burti, M. mesembrinum, M. megaloon, M. oligoon, M. geoemydae, M. georgesblanci,* and *M. megrebense,* the testes are posterior to the level of that sucker.

The first group can be divided into 2 subgroups based on the length of the intestinal ceca. In *M. sociale, M. microon, M. carli, M. leiperi, M. travassosi, M. crossophorum, M. schwetzi, M. meggitti, M. monodi, M. marrsi, M. danforthi* and *M. maroccanum,* they extend past the midlevel of the body, whereas in *M. lanceatum, M. elongatum, M. sibynomorphi,* and *M. brachyenteron,* the ceca terminate before reaching that level and usually are confined to the anterior one-third of the body.

In the subgroup with longer ceca, species are distinguished by: (1) the position of the genital pore which may be median and at the esophageal level, or posterior to the intestinal bifurcation, or lateral and anterior to that bifurcation; (2) the configuration of the vitellaria; (3) the size and shape of the cirrus pouch; (4) the length of the esophagus; (5) the relative sizes of the testes to the acetabulum; and (6) the body dimensions.

Species in the subgroup with short ceca can be separated by (1) the distribution and configuration of the vitelline follicles; (2) whether the ceca extend posterior to the testes and/or ovary; (3) the size of the cirrus pouch; and (4) whether the genital pore is anterior or posterior to the intestinal bifurcation.

In the group with the testes anterior to the acetabulum, species differ in (1) the configuration and extent of the vitellaria; (2) whether the ceca extend beyond the level of the testes and/or ovary; and (3) whether the ovary is at the level of the acetabulum or posterior to it.

Species in the third group are distinguished by: (1) the sizes of the gonads; (2) whether the genital pore is anterior or posterior to the intestinal bifurcation; (3) size of the cirrus pouch; (4) length of the esophagus and intestinal ceca; and (5) configuration and extent of the vitellaria.

Mesocoelium emend.

Diagnosis.—With characters of subfamily Mesocoeliinae (see Cheng and Provenza, 1960); genital pore either anterior or posterior to intestinal bifurcation, on or lateral to midline; testes anterior to, on same level as, or posterior to acetabulum; uterus with much folded ascending and descending limbs, folds limited to post-ovarian area; intestinal parasites of amphibians and reptiles.

Type species.—*Mesocoelium sociale* (Lühe, 1901) so designated by Odhner (1911).

After evaluating all the reported species of *Mesocoelium*, the following are considered to be valid. All measurements are given in millimeters.

Mesocoelium sociale (Lühe, 1901) Odhner, 1911
Plate I, Fig. 1

Syn. *Distomum sociale* Lühe, 1901.

Diagnosis.—Body elongate, 2.8-3.5 long, 0.7-0.72 wide; cuticle spinous, spines more conspicuous in anterior half of body; oral sucker 0.275-0.34 by 0.27-0.32, acetabulum 0.185-0.32 in diameter; prepharynx present, pharynx 0.1-0.134 by 0.065-0.098; esophagus of medium length; intestinal ceca reaching posterior one-third of body; testes, 0.17-0.24 by 0.15-0.23, at sides of acetabulum, overlapping ceca; cirrus pouch slightly longer than diameter of testes; genital pore ventral, at midlevel of esophagus; ovary posterior to right testis, 0.18-0.225 by 0.17-0.18; vitellaria of large separated follicles from lateral margins of oral sucker to tips of ceca, never intercecal; excretory vesicle Y-shaped. Eggs 0.031-0.033 by 0.02-0.023.

Type host.—*Bufo melanostictus.*

Type locality.—India (exact location not given).

Type specimen.—Not extant.

Three specimens of *M. sociale* from Montevideo, Uruguay, resemble *M. monodi.* They can be separated from that species by the larger testes which are situated on each side of the acetabulum and overlapping the ceca.

Mesocoelium sociale has been reported from *Bufo melanostictus* in Indonesia by Odhner (1911), in Calcutta, India, by Sewell (1920), from Burma by Bhalerao (1936), from Rangoon, Burma, by Chatterji (1940) and Meggitt (1927), from *Bufo* sp. in Indonesia by Bhalerao (1936), from *Rana tigrina* in Rangoon, Burma, by Meggitt (1927),

PLATE I

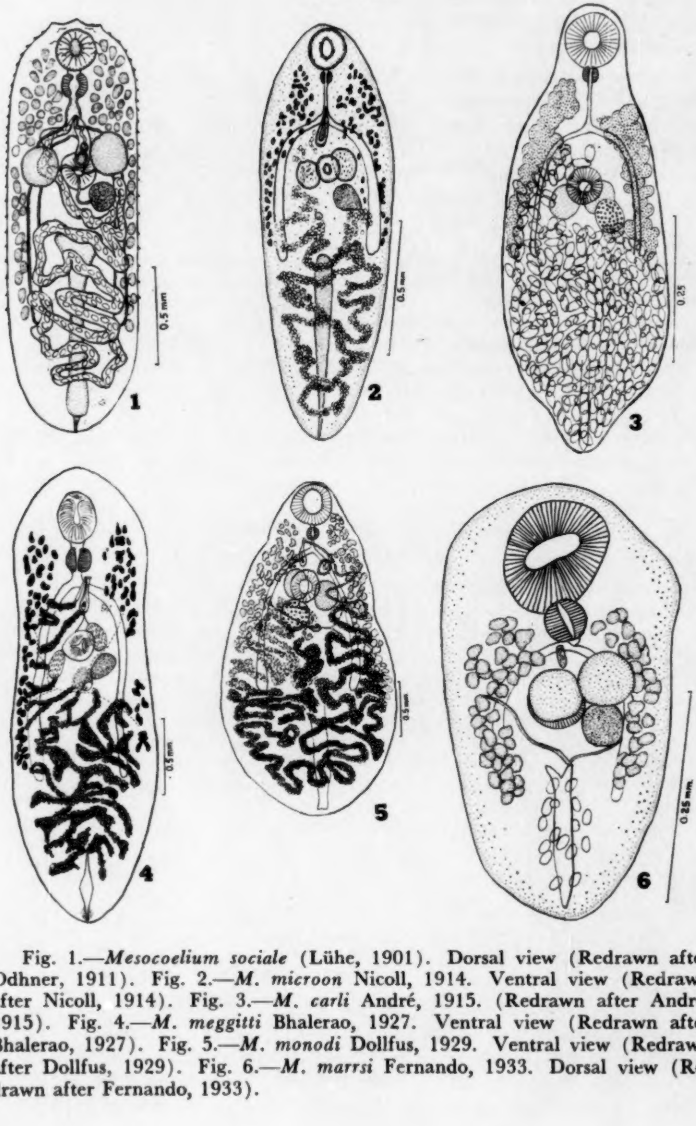


Fig. 1.—*Mesocoelium sociale* (Lühe, 1901). Dorsal view (Redrawn after Odhner, 1911). Fig. 2.—*M. microon* Nicoll, 1914. Ventral view (Redrawn after Nicoll, 1914). Fig. 3.—*M. carli* André, 1915. (Redrawn after André, 1915). Fig. 4.—*M. meggitti* Bhalerao, 1927. Ventral view (Redrawn after Bhalerao, 1927). Fig. 5.—*M. monodi* Dollfus, 1929. Ventral view (Redrawn after Dollfus, 1929). Fig. 6.—*M. marrsi* Fernando, 1933. Dorsal view (Redrawn after Fernando, 1933).

PLATE II

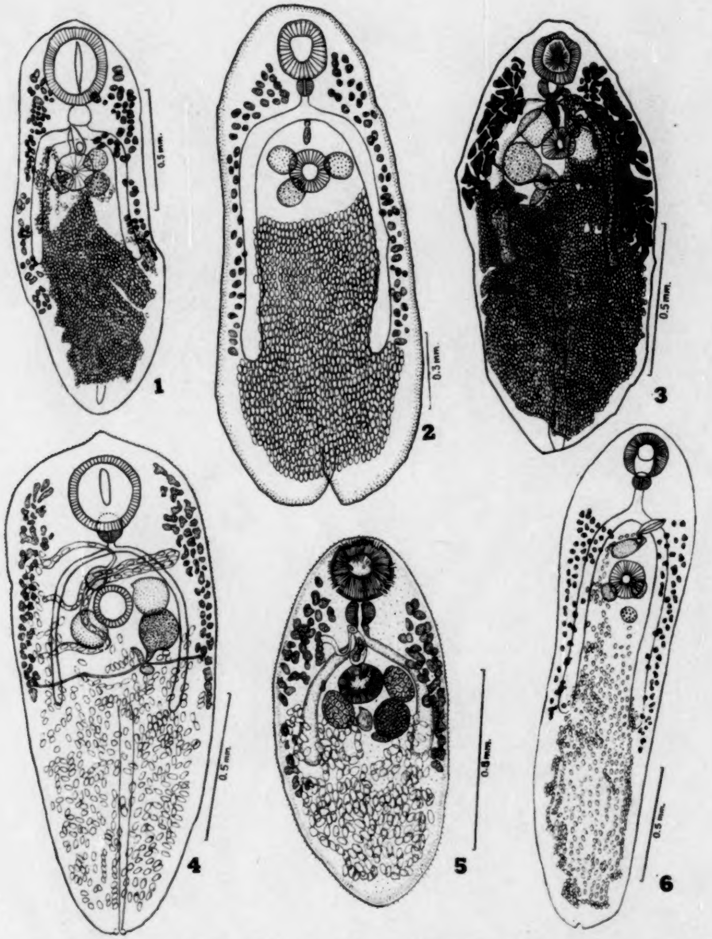


Fig. 1.—*Mesocoelium danforthi* Hoffman, 1935. Dorsal view. Camera lucida drawing of type specimen. Fig. 2.—*M. leiperi* Bhalerao, 1936. Dorsal view (Redrawn after Bhalerao, 1936). Fig. 3.—*M. travassosi* Pereira and Cuocolo, 1940. Ventral view (Redrawn after Pereira and Cuocolo, 1940). Fig. 4.—*M. mesocoelium* (Cohn, 1903) n. comb. Ventral view (Redrawn after Dollfus, 1950). Fig. 5.—*M. crossophorum* Pérez, 1942. Ventral view (Redrawn after Pérez, 1942). Fig. 6.—*M. maroccanum* Dollfus, 1951. Ventral view (Redrawn after Dollfus, 1951).

PLATE III

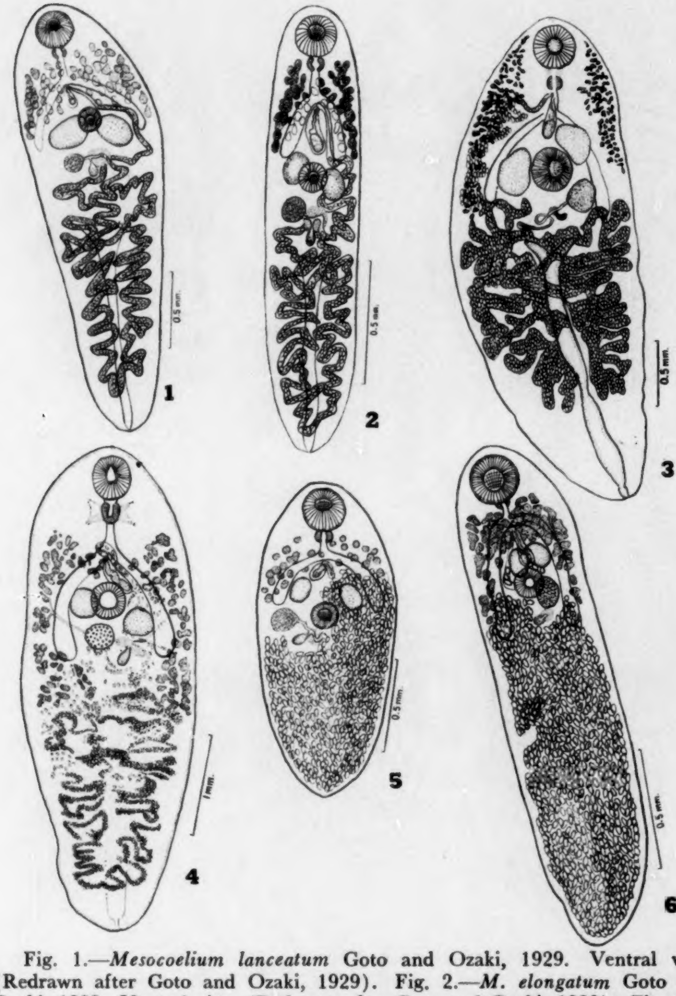


Fig. 1.—*Mesocoelium lanceatum* Goto and Ozaki, 1929. Ventral view (Redrawn after Goto and Ozaki, 1929). Fig. 2.—*M. elongatum* Goto and Ozaki, 1929. Ventral view (Redrawn after Goto and Ozaki, 1929). Fig. 3.—*M. sibynomorphi* Ruiz and Leão, 1943. Dorsal view (Redrawn after Ruiz and Leão, 1943). Fig. 4.—*M. brachyenteron* Dollfus, 1954. Ventral view (Redrawn after Dollfus, 1954). Fig. 5.—*M. ovatum* Goto and Ozaki, 1930. Ventral view (Redrawn after Goto and Ozaki, 1930). Fig. 6.—*M. japonicum* Goto and Ozaki, 1930. Dorsal view (Redrawn after Goto and Ozaki, 1930).

PLATE IV

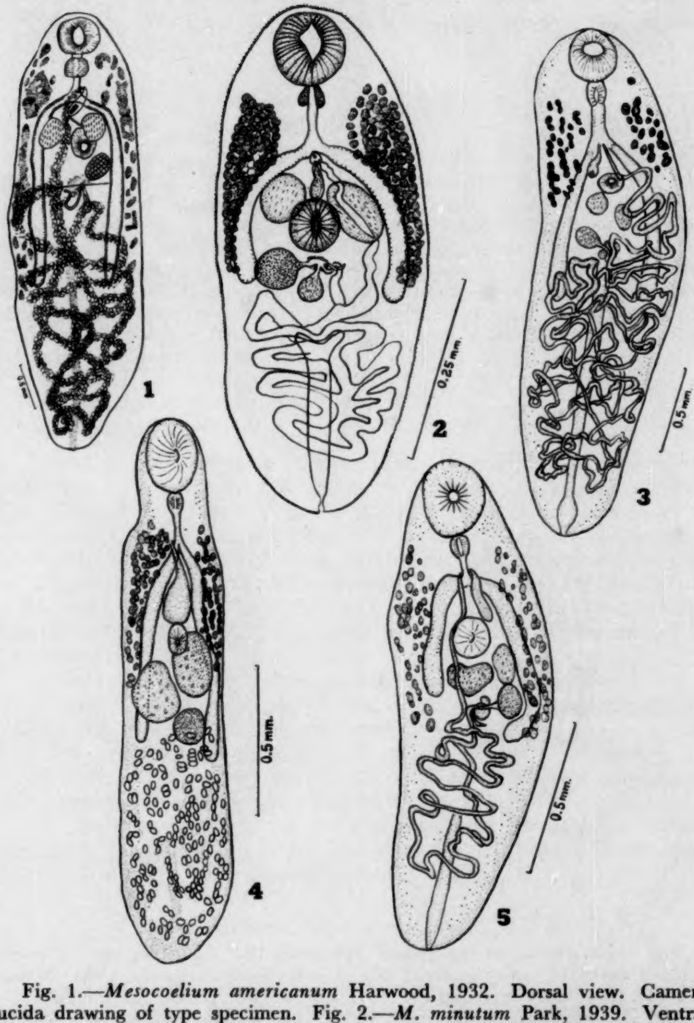


Fig. 1.—*Mesocoelium americanum* Harwood, 1932. Dorsal view. Camera lucida drawing of type specimen. Fig. 2.—*M. minutum* Park, 1939. Ventral view (Redrawn after Park, 1939). Fig. 3.—*M. mesembrinum* Johnston, 1912. Dorsal view (Redrawn after Johnston, 1912). Fig. 4.—*M. megaloon* Johnston, 1912. Ventral view (Redrawn after Johnston, 1912). Fig. 5.—*M. oligoon* Johnston, 1912. Dorsal view (Redrawn after Johnston, 1912).

PLATE V

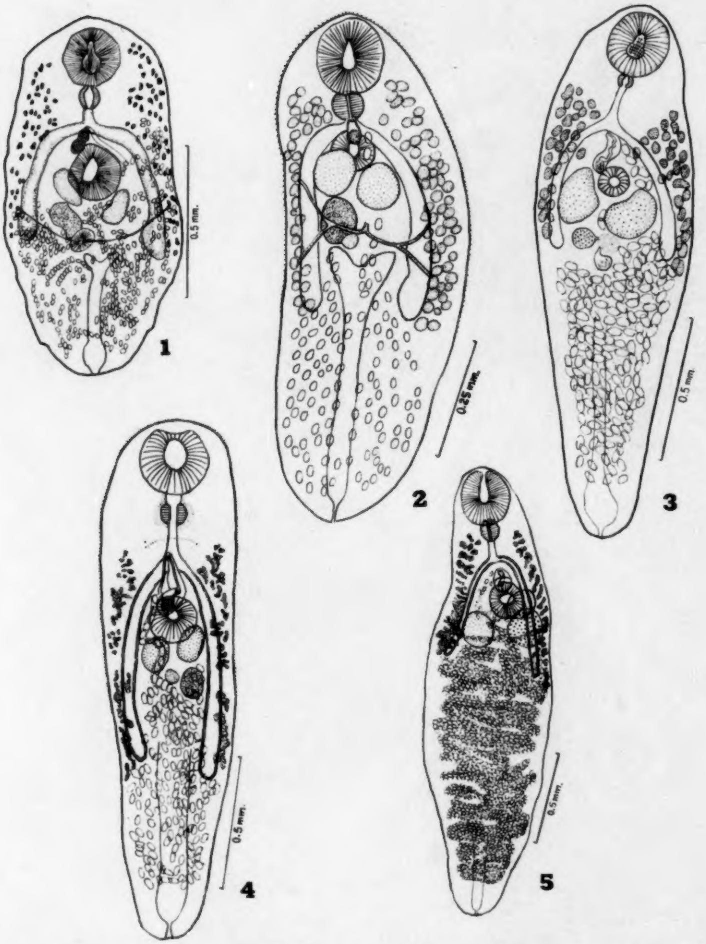


Fig. 1.—*Mesocoelium incognitum* Travassos, 1921. Ventral view. Camera lucida drawing of type specimen. Fig. 2.—*M. burti* Fernando, 1933. Dorsal view (Redrawn after Fernando, 1933). Fig. 3.—*M. geoemydae* Ozaki, 1935. Ventral view (Redrawn after Ozaki, 1935). Fig. 4.—*M. georgesblanci* Dollfus, 1954. Ventral view (Redrawn after Dollfus, 1954). Fig. 5.—*M. magrebense* Dollfus, 1954. Ventral view (Redrawn after Dollfus, 1954).

from *Ptyas mucosus* in Rangoon, Burma, by Chatterji (1940), and from *Bufo crucifer* in Brazil by Travassos (1924).

Sewell (1920) reported the flame-cell pattern of this species to be 2 [(3+3+3) + (3+3+3)] which Faust (1932) gave as the pattern in the Dicrocoeliidae.

Mesocoelium mesembrinum Johnston, 1912
Plate IV, Fig. 3

Diagnosis. — Body elongate, 2.3-3.7 long, 0.89-1.6 wide; entire cuticle spinous; oral sucker 0.293 in diameter; acetabulum 0.196 in diameter; prepharynx not observed; esophagus of medium length; intestinal ceca reaching midlevel of body; testes oval, 0.195 in greatest diameter, posterior to acetabulum, oblique, with right testis slightly more anterior; cirrus pouch approximately as long as testes; genital pore ventral at intestinal bifurcation; ovary, 0.163 in greatest diameter, posterior to right testis; vitellaria of small separated follicles in lateral fields from level of pharynx to that of testes, never posterior to ovary; excretory vesicle I-shaped, extending to level of seminal receptacle. Eggs averaging 0.04 long by 0.025 wide.

Type host.—*Hyla caerulea.*

Type locality.—Nouveau Galles du Sud, Australia.

Type specimen.—Australian Museum Coll. No. W-341.

In the author's opinion, *Mesocoelium mesembrinum* is not synonymous with *M. oligoon* as considered by Pereira and Cuocolo (1940). The distribution of the vitellaria of *M. mesembrinum* is limited to areas lateral to the ceca from the level of the pharynx to the anterior one-fourth of the intestinal ceca; that of *M. oligoon* is also lateral to the ceca, but extends posteriorly beyond the cecal tips. The left cecum of *M. oligoon* is longer than the right while the ceca of *M. mesembrinum* are of equal length. For these reasons the 2 species should be considered distinct.

Mesocoelium mesembrinum is similar to *M. georgesblanci,* but is distinguished from that species by the disposition of its vitellaria. The follicles are extracecal along the anterior one-third of the ceca and not along the entire lengths as in *M. georgesblanci.* Furthermore, the acetabulum, cirrus pouch, and gonads of *M. mesembrinum* are smaller and a conspicuous prepharynx is absent.

The only other record for the distribution of *M. mesembrinum* is that of T. H. Johnston (1916) who reported this species in the same host at Brisbane, Queensland, Australia.

Mesocoelium megaloon Johnston, 1912
Plate IV, Fig. 4

Diagnosis.—Body elongate, averaging 1.8 long, 0.358 wide; cuticle aspinous; oral sucker 0.194 in diameter, acetabulum 0.065 in diameter; prepharynx absent, esophagus moderately long, intestinal ceca extending into middle one-third of body; testes irregularly oval, averaging 0.182 by 0.129, slightly obliquely arranged, overlapping ceca laterally; right testis slightly more anterior and overlapping acetabulum dorsally; ovary subspherical, averaging 0.112 in diam-

eter, immediately behind and slightly to right of left testis; cirrus pouch, approximately twice the size of acetabulum, filling intercecal space anterior to acetabulum; genital pore on midline anterior to intestinal bifurcation; vitelline glands in lateral fields from level of esophagus to that of testes; excretory vesicle Y-shaped. Eggs 0.043-0.052 by 0.029.

Type host.—*Hyla ewingii.*

Type locality.—Sydney, Australia.

Type specimen.—Australian Museum Coll. No. W-343.

Mesocoelium megaloon appears to be most closely related to *M. georgesblanci,* which, however, has large testes (0.181 by 0.129) that overlap the ceca.

Mesocoelium oligoon Johnston, 1912
Plate IV, Fig. 5

Diagnosis.—Body elongate, averaging 1.53 long, 0.59 wide; cuticle sparsely covered with spines; oral sucker 0.215 in diameter, acetabulum 0.129 in diameter; esophagus of medium length; intestinal ceca unequal, left cecum extending posterior to level of ovary, right cecum reaching only to level of testes; testes irregularly oval or "polyhedral," averaging 0.165 by 0.099, side by side in intercecal region posterior to acetabulum; cirrus pouch long, slender, approximately as long as diameter of acetabulum; ovary oval, 0.133 by 0.09, situated posterior to left testis; vitelline follicles, 0.028-0.032 long, comparatively numerous, about 70 on each side, extending from level of pharynx to beyond tip of right cecum and to tips of left cecum; excretory vesicle I-shaped extending anteriorly through posterior one-fourth of body length. Eggs 0.039-0.052 by 0.028.

Type host.—*Hyla citropus.*

Type locality.—Lodden River (near Bulli), New South Wales, Australia.

Type specimen.—Australian Museum Coll. No. W-342.

Mesocoelium oligoon most closely resembles *M. megaloon,* but can be distinguished from the latter by its ceca which are characteristically unequal in length, by its testes which are smaller and which do not overlap the ceca, by its vitellarial configuration in extending along the entire lengths of the ceca and sometimes beyond them, and by its smaller cirrus pouch which does not occupy the entire intercecal space anterior to the acetabulum.

Mesocoelium microon Nicoll, 1914
Plate I, Fig. 2

Diagnosis.—Body elongate oval, 1-3.5 long, 0.77 wide; cuticle more spinous towards anterior end of body; oral sucker averaging 0.25 in diameter, acetabulum averaging 0.18 in diameter; no prepharynx reported, pharynx 0.08 in diameter, esophagus approximately twice the length of pharynx, intestinal ceca reaching past midlength of body, testes irregularly oval, 0.21 by 0.14, on same level as acetabulum, partially overlapping it dorsally along their median borders; cirrus sac slender, length approximates greatest diameter of testes; ovary posterior to left testis, averaging 0.15 in diameter; vitellaria of comparatively small follicles, laterally situated, from level of pharynx to cecal tips. Nicoll (1914) stated that the extent of the follicles were viable and may be

completely absent on one side posterior to acetabulum. Excretory vesicle I-shape extending anteriorly to midlength of body. Eggs 0.033-0.041 by 0.024-0.028.

Type hosts.—*Hyla coerulea, H. gracilenta* and *Tiliqua scincoides.*[1]

Type locality.—North Queensland, Australia.

Type specimen.—Unknown.

The author is not in agreement with Pereira and Cuocolo (1940) who considered *M. microon* as synonymous with *M. oligoon.* Examination of the original descriptions and plates by Johnston (1912) and Nicoll (1914) indicates that *M. microon* can be separated from *M. oligoon* by the position of the testes on the same level and on each side of the acetabulum in *M. microon* and by the equal length of the intestinal ceca. In *M. oligoon* the irregularly shaped testes are posterior to the acetabulum and the ceca are of unequal length. Until further evidence indicates differently, *M. microon* and *M. oligoon* must be considered distinct species.

Mesocoelium microon most closely resembles *M. carli, M. crossophorum,* and *M. monodi,* but it can be distinguished from *M. carli* by the extremely small independently follicular vitellaria, and by the position of its testes on the same level as the acetabulum. In *M. carli* the vitelline follicles are large and fused to form a continuous band; the testes are partially posterior to the acetabulum. *M. microon* can be distinguished from *M. crossophorum* by the medially placed genital pore anterior to the cecal bifurcation; by the smaller ovary which is not larger than the testes; and by the absence of refractile spicules along the anterior and lateral margins of the oral sucker. In *M. crossophorum* the genital pore is on the right of the esophagus and the ovary is larger than the testes.

Mesocoelium carli André, 1915
Plate I, Fig. 3

Diagnosis.—Body elongate, narrow at anterior and posterior ends; 0.88 long, 0.28 wide; oral sucker 0.086-0.095 in diameter, acetabulum 0.05-0.068 in diameter; no prepharynx observed, pharynx 0.025 in diameter; esophagus 2 to 3 times as long as pharynx; intestinal ceca extending to, or slightly posterior to midlength of body; testes globular, approximately same size as acetabulum, partially posterior to it and overlapping it along their anteromedial borders; ovary approximately same size as testes, posterior to and partially overlapping left testis; vitellaria extensive, follicles large, forming two continuous masses along extent of esophagus and ceca. André (1915) reported that the compact vitellaria may extend medially into the intercecal zone. Excretory vesicle Y-shape. Eggs 0.037-0.047 by 0.022-0.026.

Type host.—*Cinixys belliana.*

Type locality.—Busu, Uganda, Africa.

[1] Nicoll (1914) reported *M. microon* as very common in the 3 hosts in North Queensland, Australia; a single host usually possessed 10-40 parasites in its duodenum; but he failed to mention from which of the 3 hosts the type specimen was recovered, hence all 3 are listed as the "type hosts."

Type specimen.—Not extant.

Other specimens.—Helminth. Coll., Museum of Natural History, Paris, France.

Mesocoelium carli most closely resembles *M. microon,* but it can be distinguished from the latter by its large, compactly fused vitelline glands. In *M. microon* the vitelline follicles are small and distinct.

Dollfus (1950) reported this species in *Cinixys erosa* from Port-Gentil, Gabon, Africa.

Mesocoelium incognitum Travassos, 1921
Plate V, Fig. 1

Syn. *Mesocoelium waltoni* Pereira and Cuocolo, 1940.

Diagnosis.—Body elongate, 1.151-1.249 long, 0.5-0.9 wide; cuticle beset with spines in anterior half or two-thirds of body; oral sucker 0.14-0.25 in diameter, acetabulum 0.16-0.3 in diameter; no prepharynx, pharynx 0.06-0.1 in diameter; esophagus short, less than length of pharynx; intestinal ceca reaching posterior one-third of body; testes irregularly oval, close to and posterior to acetabulum, right testis, 0.062-0.18 by 0.053-0.101, slightly anterior to left, left testis 0.08-0.164 by 0.049-0.113; cirrus pouch small, approximately half the diameter of acetabulum in length; ovary irregularly oval, 0.082-0.2 by 0.049-0.147, posterior to left or right testis; vitelline follicles small and sparsely arranged, from lateral borders of oral suckers to cecal tips; excretory vesicle Y-shape, extending to level of cecal tips. Eggs 0.037-0.041 by 0.021-0.025.

Type host.—*Bufo marinus.*

Type locality.—Guaratinguetá, Brazil.

Type specimen.—Helminth. Coll. Institudo Oswaldo Cruz, San Paulo, Brazil.

Four specimens of this species from Sao Paulo, Brazil, were studied.

Pereira and Cuocolo (1940) described *Mesocoelium waltoni* from the intestine of *Bufo marinus* captured at San Paulo, Brazil. These authors stated that *M. waltoni* closely resembles *M. megaloon* Johnston, 1912, and *M. carli* André, 1915. However, the species can be easily distinguished from one another by the sizes and arrangements of the vitelline follicles, which are larger and more compact in *M. carli,* medium-sized and not compact in *M. megaloon,* and extremely small and comparatively more sparse in *M. waltoni.* Furthermore, the relative positions of the testes and ovary also serve as diagnostic characteristics. Further study revealed that *M. waltoni* is identical with *M. incognitum* Travassos, 1921. The dimensions of the body, suckers, gonads and other internal organs vary within the same size range. The relative positions of the internal organs, the configuration of the vitellaria, and the type of excretory vesicle, are all identical, even the positions of the cornual bifurcation of the Y-shaped excretory vesicle. The fact that both were recovered from the same host, *Bufo marinus,* from Brazil, further suggests the probability of their being identical.

Mesocoelium incognitum most closely resembles *M. geoemydae* although the morphological similarity is not great. *M. incognitum* (body length 1.15 - 1.25 mm) is shorter than *M. geoemydae* (body

length 1.55 - 1.85 mm); the diameter of the acetabulum of *M. incognitum* may be as large as 0.3 mm, while that of *M. geoemydae* is never larger than 0.12 mm; and the vitelline follicles of *M. incognitum* are extremely small and are scattered in the lateral fields in the anterior two-thirds of the body, while those of *M. geoemydae* are larger in size and are limited to the region along the lateral margins of the ceca.

The only other record of *Mesocoelium incognitum* is that of Travassos (1924) in *Bufo crucifer* from San Paulo, Brazil.

Mesocoelium meggitti Bhalerao, 1927
Plate I, Fig. 4

Diagnosis.—Body elongate, broa er anteriorly than posteriorly, 1.02-3.3 long, 0.36-1.03 wide; cuticle spinous in anterior half or two-thirds of body; anterior sucker 0.14-0.27 in diameter, ventral sucker 0.07-0.17 in diameter; prepharynx present, pharynx 0.05-0.1 by 0.06-0.13, esophagus short, 0.02-0.08 in length; intestinal ceca reaching posterior one-third of body; testes oval, 0.08-0.2 by 0.07-0.15, one anterior to its mate, on each side of acetabulum; cirrus pouch small, 0.23 by 0.10; genital pore at midlength of esophagus but to left of midline, ovary suboval, 0.08-0.2 by 0.07-0.15, posterior to anteriormost testis; vitelline glands singularly follicular, lateral, from level of anterior sucker to near ends of ceca; excretory vesicle I-shape. Eggs 0.03-0.036 by 0.02-0.024.

Type host.—*Mabuia dissimilis.*

Type locality.—Rangoon, Burma.

Type specimen.—Unknown.

Chatterji (1931) reported this parasite from the same host from India, while Tubangui (1931) reported *M. meggitti* in *Mabuia multifasciata* from Los Ranos, Philippine Islands.

Mesocoelium meggitti most closely resembles *M. maroccanum.* Both species possess a genital pore which opens ventrally to the left of the median line; however, *M. meggitti* can be distinguished from *M. maroccanum* by its larger gonads, the greatest diameter of the testes is subequal to that of the acetabulum, while the ovary is as large, if not larger, than the testes. In *M. maroccanum* the testes are approximately one-fourth the size of the acetabulum, and the ovary is proportionally smaller.

Mesocoelium lanceatum Goto and Ozaki, 1929
Plate III, Fig. 1

Syns. *Mesocoelium brevicaecum* Ochi, 1930.
Mesocoelium pearsei Goto and Ozaki, 1930.

Diagnosis.—Body lanceolate, narrower at posterior end, 2.0-3.3 long, 0.52-0.95 wide; cuticle spinous in anterior half of body; oral sucker 0.22-0.33 in diameter, acetabulum, 0.15-0.24 in diameter, situated in anterior one-fourth of body; prepharynx very short, pharynx 0.07-0.09 in diameter, esophagus 0.18-0.24 long; intestinal ceca comparatively short, only reaching level of posterior margins of testes; testes suboval, 0.10-0.29 by 0.07-0.22. on same place and on each side of acetabulum, partially overlapping the latter; ovary, 0.12-0.17 in diameter, posterior to right testis; cirrus pouch small, 0.021-0.027 by

0.08-0.1; vitellaria of singular follicles mainly lateral to esophagus and ceca but some follicles intermingle along medial line; excretory vesicle Y-shape. Eggs 0.04-0.051 by 0.023-0.031.

Type host.—*Tylototriton andersoni.*

Type locality.—Hyukyu Islands, Japan.

Type specimen.—Not available.

Goto and Ozaki (1929) first mentioned *Mesocoelium brevicaecum* (*nomen nudum*) which was not described until 1930 by Ochi from the intestine of *Bufo vulgaris formosus* from Hiroshima and Otsu, Japan. Ono (1930) reported this species in the same host and also in *Elapha quadrivirgata* and *Rana catesbiana,* captured at Onomichi, Japan; and Yamaguti (1936) reported *M. brevicaecum* from the type host at Kyoto, Japan.

The author believes that *M. brevicaecum* should be considered synonymous with *M. lanceatum* Goto and Ozaki, 1929. The body dimensions of the two species fall within the same range; the arrangement of the cuticular spines are identical. The testes of *M. brevicaecum* (0.10 - 0.24 by 0.07 - 0.10 mm) are slightly smaller than that of *M. lanceatum* (0.2 - 0.29 by 0.2 - 0.22 mm), but the greater dimension is in width only and the difference is insignificant; the ovaries are within the same range and so are the eggs. The distribution of the vitellaria are similar and both species have the Y-type excretory vesicle. Goto and Ozaki (1929) realized the great similarity between the two species and apparently had knowledge of the existence of Ochi's specimens, but erected *M. lanceatum* based on differences in body outline, ratio of suckers and coiling of the uterine limbs. These highly variable characteristics can all be attributed to the degree of contraction during fixation.

Ochi (1930) reported the life cycle of *M. brevicaecum* (=*M. lanceatum*). The fluke utilizes only one intermediate host, the land snail, *Euhadra quaesita* (Deshayes), and the cercaria, in the molluscan host, develops into an unencysted metacercaria for which Ochi used the term "adoluscaria." This life history pattern is essentially identical to that of *Brachycoelium obesum* Nicoll, 1914 (Cheng, 1960). This information serves as further evidence that *Mesocoelium* and *Brachycoelium* are closely related. In a report of the life history of *Glypthelmins quieta,* Rankin (1944) pointed out the phylogenetic proximity of *Glypthelmins* to *Brachycoelium* and hence also to *Mesocoelium.* The parallel life cycles must be considered of great importance and strong evidence for the grouping of these genera under the independent family, Brachycoeliidae.

Pereira and Cuocolo (1940) considered *M. brevicaecum* and *M. ovatum* both synonymous with *M. elongatum.* The author is not in agreement with these designations since *M. brevicaecum* (=*M. lanceatum*) can be easily separated from *M. ovatum* by the relative sizes of their gonads. In *M. brevicaecum* the testes are approximately one-third the size of the acetabulum and are situated on each side of it, while in *M. elongatum* they are similarly situated but are approxi-

mately the same size as the acetabulum; furthermore, the cirrus pouch of *M. brevicaecum* is as long as the diameter of the acetabulum, while in *M. elongatum* the cirrus pouch is approximately twice as long as the diameter of the acetabulum.

M. ovatum differs from *M. elongatum* by its smaller cirrus pouch the length of which is approximately two-thirds the diameter of the acetabulum; by the position of its testes, distinctly anterior to the acetabulum. In *M. elongatum* the length of the cirrus pouch is approximately twice the diameter of the acetabulum, and the testes are approximately the same size (and on the same level) as the acetabulum.

Until further evidence can be provided through life history studies, these morphological differences must suffice in the retention of *M. ovatum* and *M. elongatum* as distinct species and, for the reasons given above, *M. brevicaecum* is considered a synonym of *M. lanceatum*.

In 1930 Goto and Ozaki described *Mesocoelium pearsei* from the small intestine of *Pseudosalamandra stejnegeri* (Dunn) from Kagoshima, Japan. They stated that this species is closely related to *M. elongatum* Goto and Ozaki, 1929, but could be distinguished from it in that "the body is somewhat broader, the oral sucker and the acetabulum are closer to each other, and the intestinal ceca extend beyond the acetabulum." These characteristics are among those which separates *M. lanceatum* from *M. elongatum*. The author is of the opinion that *M. pearsei* is identical with *M. lanceatum*. The body dimensions of the two species fall within the same range; the alimentary tracts appear to be identical; the gonads and related structures are situated in identical positions; however, the testes of *M. pearsei* are slightly smaller than those of *M. lanceatum* (a difference of 0.07 mm which may be attributed to the differences in pressure during fixation) but this can hardly be considered valid as a species characteristic. Furthermore, the vitellarial patterns, positions of the genital pores, sizes and positions of the suckers and the dimensions of the eggs are all comparable. For these reasons the author considers *M. pearsei* synonymous with *M. lanceatum*.

Pereira and Cuocolo (1940) suggested that *M. pearsei* is synonymous with *M. japonicum*, a decision based on morphological similarities. The author does not agree since the two can be easily distinguished by the intestinal ceca which extend posterior to the level of the ovary in *M. japonicum* and are shorter in *M. pearsei*. Furthermore, the testes of *M. pearsei* are on the same level as the acetabulum while those of *M. japonicum* are anterior to the acetabulum. For these reasons, the author does not accept Pereira and Cuocolo's designation, but, as indicated above, considers *M. pearsei* a synonym of *M. lanceatum*.

Mesocoelium lanceatum most closely resembles *M. brachyenteron*. It can be separated from the latter by its shorter intestinal ceca which do not extend beyond the level of the testes as they do in *M. brachy-*

enteron. Furthermore, the vitellaria of *M. lanceatum* are confluent in the median line, a condition not found in *M. branchyenteron.*

Mesocoelium elongatum Goto and Ozaki, 1929
Plate III, Fig. 2

Diagnosis.—Body elongate, 1.78-1.82 long, 0.42-0.46 wide; anterior half of body spinous; oral sucker 0.2-0.25 in diameter, acetabulum, 0.17 in diameter, in anterior part of middle one-third of body; no prepharynx, pharynx 0.065 in diameter, esophagus 0.11 long; intestinal ceca short, only reaching anterior margins of testes; testes oval, 0.10-0.14 by 0.09-0.12, on each side of acetabulum and partially overlapping it; cirrus pouch large, 0.13 by 0.05; ovary, 0.10-0.11 in diameter, posterior to right testis; vitellaria lateral, along lengths of esophagus and intestinal ceca with few follicles overlying them; excretory vesicle Y-shape, bifurcating posterior to ovary. Eggs 0.04-0.043 by 0.025- 0.027.

Type host.—*Diemyctylus pyrrhogaster.*

Type localities.—Hiroshima, Sendai, Tokyo, Japan.[2]

Type specimen.—Not recorded.

Pearse (1932) and Yamaguti (1936) reported this species from the same host; Yamaguti reported it from Siga, Japan, while Pearse did not give the exact location in Japan. Yamaguti (*ibid.*) also reported *Mesocoelium elongatum* in *Rana rugosa* from Siga, Japan, and Ozaki (1936) reported it in *Geoemyda spengleri* from Loochow Island, Japan.

Mesocoelium elongatum most closely resembles *M. lanceatum,* however, it can be distinguished from the latter by its shorter intestinal ceca which are the shortest among all the members of the genus. The ceca do not even reach the level of the testes in *M. elongatum* while they do in *M. lanceatum.*

Mesocoelium monodi Dollfus, 1929
Plate I, Fig. 5

Diagnosis.—Body pear-shaped, wider at posterior end, averaging 3.0 long, 1.5 wide; cuticle completely spinous, more so in anterior half of body; oral sucker 0.34-0.37 in diameter, acetabulum 0.265 in diameter; short prepharynx, pharynx and short esophagus (0.125) present; intestinal ceca reaching anterior border of posterior one-third of body; testes rounded, 0.2-0.28 in diameter, on each side of acetabulum, partially overlapping it; cirrus pouch 0.21-0.24 by 0.08-0.1; genital pore at midlength of esophagus but to right of midline; ovary, 0.225-0.3, situated posterior to right testis; vitelline follicles of small and distinct units, lateral along the prepharynx, pharynx, esophagus and ceca; shape of excretory vesicle not observed. Eggs 0.035-0.038 by 0.02-0.023.

Type host.—*Chamaeleon gracilis.*

Type locality.—Souelaba, Cameron, North Africa.

Type specimen.—Museum of Natural History, Paris, France.

---

[2] Goto and Ozaki (1929) reported *Mesocoelium elongatum* from the intestine of *Diemyctylus pyrrhogaster* collected at Hiroshima, Sendai and Tokyo, Japan, but did not indicate from which locality the type specimen was obtained, hence all three localities are listed as the "type localities."

Szidat (1932) reported *Mesocoelium monodi* in *Rana mascarenien-sis, Bufo regularis, Agama colonorium, Agama planiceps, Lygosoma fernandi,* and *Mabuia maculilabrus* from Liberia, Africa, and Baylis (1939) reported this species from *Chamaeleon etiennei* from the Valley of River Kwanga, Belgium Congo, Africa.

Mesocoelium monodi most closely resembles *M. crossophorum;* both species possess genital pores which are situated to the right of the median line. However, *M. monodi* can be separated from *M. crossophorum* by the lack of refractile spicules along its anterior sucker margins, and by its more medially placed testes which overlap the acetabulum dorsally.

Mesocoelium ovatum Goto and Ozaki, 1930
Plate III, Fig. 5

Diagnosis.—Body oval, 1.62-1.7 long, 0.62-0.65 wide; anterior half of body spinous; oral sucker 0.22-0.23 in diameter, acetabulum approximately 2/3 size of oral sucker; no prepharynx, pharynx 0.06 in diameter, and esophagus 0.045 long; intestinal ceca reaching beyond testes; testes oval, 0.15 by 0.11, anterior to acetabulum; cirrus pouch 0.09-0.12 by 0.06-0.08; ovary, 0.12-0.13 in diameter, behind right testis; vitelline follicles singularly follicular, main bodies of which are laterad to ceca with few follicles confluent in median line; excretory vesicle Y-shape. Eggs 0.038-0.04 by 0.024-0.026.

Type host.—*Rana rugosa.*
Type locality.—Sendai, Japan.
Type specimen.—Unknown.

Mesocoelium ovatum is probably most closely related to *M. minutum* and *M. japonicum.* It can be distinguished from *M. minutum* by its shorter intestinal ceca which extend only to the level of the anterior margin of the acetabulum and not beyond the acetabulum as in *M. minutum.* Furthermore, the ovary of *M. ovatum* is on the same level as the acetabulum while that of *M. minutum* is posterior to the acetabulum; the vitelline follicles of *M. ovatum* are few in number, with a few follicles from each side intermingling along the medial line; in *M. minutum* the follicles are numerous and are limited to the two lateral fields; finally, the body dimensions of *M. ovatum* (1.62-1.7 by 0.62 - 0.65 mm) are approximately three times as large as those of *M. minutum* (0.554 - 1.159 by 0.26 - 0.398 mm).

M. ovatum can be distinguished from *M. japonicum* by its fewer vitelline follicles; the shorter intestinal ceca which do not extend beyond the level of the acetabulum as in *M. japonicum;* by its body length (1.62 - 1.7 mm) which is considerably shorter than that of *M. japonicum* (2.0 - 2.3 mm); by the position of its ovary which is on the same level as the acetabulum and not partially posterior to it as in *M. japonicum;* and by the spacial relationship of its testes which are not in contact with each other as in *M. japonicum,* but lie on each side and anterior to the acetabulum.

Mesocoelium japonicum Goto and Ozaki, 1930
Plate III, Fig. 6

Diagnosis.—Body elongate, 2.0-2.3 long, 0.85-0.95 wide; cuticle spinous in anterior half of body; oral sucker 0.24-0.28 in diameter, acetabulum 0.15-0.19 in diameter; no prepharynx, pharynx 0.055 in diameter, esophagus short; intestinal ceca reaching past ovary but terminating in anterior one-third of body; testes oval, 0.14-0.17 in greatest diameter, anterior to acetabulum, touching each other medially; cirrus pouch large, 0.2 by 0.9; ovary oval, 0.15-0.21 in greatest diameter, partially posterior to acetabulum behind left testis; vitelline follicles of irregularly shaped, laterally situated acini along lengths of esophagus and intestinal ceca, and with many follicles confluent medially; excretory vesicle Y-shape (?). Eggs 0.045-0.049 by 0.026-0.03.

Type host.—*Polypedates buergeri.*

Type locality.—Yasuhara, Japan.

Type specimen.—Unknown.

Goto and Ozaki (1930) also reported this species in *Pseudosalamandra stejnegeri* from Kyushu, Japan.

Mesocoelium japonicum is most similar to *M. minutum* but can be distinguished from the latter by the configuration of the vitellaria which are confluent medially, a condition not found in *M. minutum;* by its body dimensions (2.0 - 2.3 by 0.85 - 0.95 mm) which are 2 to 3 times greater than those of *M. minutum* (0.554 - 1.159 by 0.26 - 0.308 mm); and by the relative sizes of the testes which in *M. japonicum* are smaller than the acetabulum and which in *M. minutum* are as large or larger than the acetabulum.

Mesocoelium americanum Harwood, 1932
Plate IV, Fig. 1

Diagnosis.—Body elongate, 1.2-2 long, 0.5-0.7 wide; cuticle spinous in cephalic region; oral sucker 0.21-0.27 in diameter, acetabulum 0.13-0.2 in diameter, esophagus short, never longer than pharynx; intestinal ceca extending to anterior margin of posterior one-third of body; testes irregularly oval, 0.07-0.14 by 0.105-0.15, partially anterior to acetabulum; length of cirrus pouch subequal to diameter of acetabulum; genital pore midway between cecal bifurcation and pharynx, to left of midline; ovary, 0.084-0.14 by 0.092-0.18, posterior to acetabulum and behind left testis; vitellaria lateral, of unequal-sized follicles, extending beyond cecal tips; excretory vesicle I-shape. Eggs 0.02-0.031 by 0.038-0.044.

Type host.—*Storeria dekayi.*[3]

Type locality.—Houston, Texas.

Type specimen.—USNM Helminth Coll. No. *30868;* paratype Coll. No. *30869.*

The type and paratype specimens were studied. *Mesocoelium americanum* is most similar to *M. japonicum* and *M. minutum,* however,

[3] Harwood (1932) recorded *M. americanum* from three hosts, *Storeria dekayi, Leiolopisma laterale* and *Eumeces fasciatus,* but did not specify from which of these the type specimen was recovered. The type specimen, however, is marked to have been recovered from *Storeria dekayi.*

it can be distinguished from these species by its longer intestinal ceca which extend to the anterior margin of the posterior one-third of the body; by the presence of a conspicuous prepharynx; and by the position of its genital pore which is lateral and to the right of the midline in the area of the esophagus. In *M. japonicum* and *M. minutum* the genital pore lies between the ceca, a short distance posterior to the cecal bifurcation.

Mesocoelium burti Fernando, 1933
Plate V, Fig. 2

Diagnosis.—Body elongate, 0.98-1.06 long, 0.45-0.53 wide; cuticle spinous; oral sucker averaging 0.175 in diameter, acetabulum, averaging 0.131 in diameter, posterior to and adjacent to cecal bifurcation; no prepharynx, pharynx 0.06 in diameter, esophagus extremely short; intestinal ceca extending posterior to midlength of body; testes rounded, averaging 0.14-0.122, immediately posterior to acetabulum, left one slightly anterior to right; cirrus pouch short, partially overlapping acetabulum; ovary oval, 0.152 by 0.078, posterior to left testis; vitelline follicles uniform in size, lateral in position, extending to cecal tips; excretory vesicle Y-shape, extending anteriorly to level of cecal tips. Eggs 0.035-0.036 by 0.019-0.022.

Type host.— *Rhacophorus maculatus.*
Type locality.—Colombo, Ceylon.
Type specimen.—British Museum of Natural History.

Pereira and Cuocolo (1940) postulated that *M. burti* represents the young of *M. marrsi* and hence considered the former synonymous with *M. marrsi.* This postulation was made without evidence from life history studies of either species and these workers did not indicate that they had examined young specimens of *M. marrsi.* Morphologically the two species can be separated by the relative size and position of their gonads. In *M. marrsi* the testes are on the same level as the acetabulum and their diameters approximate that of the acetabulum; in *M. burti* the testes are posterior to the acetabulum. Furthermore, the acetabulum of *M. burti* is in the intercecal space immediately posterior to the cecal bifurcation while that of *M. marrsi* is more posteriorly located. The specimens of both species as described by Fernando (1933) contained eggs in their uteri. Since the members of *Mesocoelium* are known not to be progenetic, it must be assumed that the specimens are all mature, hence the writer considers *M. burti* and *M. marrsi* as distinct species.

The similarity of *M. burti* to *M. incognitum, M. mesembrinum, M. oligoon, M. geoemydae* and *M. magrebense* is approximately equal and it can be distinguished from these species by its comparatively short and wide cirrus pouch, and by the position of its acetabulum which lies anteriorly in the intracecal space, touching the medial margins of the ceca and the posterior margin of the cecal bifurcation, a condition not found in any other species of *Mesocoelium.*

Mesocoelium marrsi Fernando, 1933
Plate I, Fig. 6

Diagnosis.—Body irregularly oval, 0.52 long, 0.312 wide; cuticle aspinous; oral sucker averaging 0.148 by 0.131; acetabulum in middle of body, 0.105 in diameter; prepharynx short, pharynx 0.061 in diameter, esophagus extremely short; intestinal ceca reaching posterior one-third of body; testes globular, 0.098-0.113 by 0.073-0.087, left testis in middle of body, overlapping acetabulum, right testis overlapping cecum and touching its mate; cirrus pouch small, approximately one-third the diameter of testes in length; ovary, 0.105 by 0.078, posterior to but in contact with right testis; all vitelline follicles of subequal dimensions, extending along lengths of ceca between and lateral to them; excretory vesicle Y-shape with the point of bifurcation lying anterior to level of cecal tips. Eggs few, limited to posterior one-third of body, averaging 0.035 by 0.022.

Type host.—*Rhacophorus eques.*

Type locality.—Ohiyu, Ceylon.

Type specimen.—British Museum of Natural History.

Mesocoelium marrsi most closely resembles *M. monodi*, however, it can be separated from the latter by its body length which is approximately one-sixth as long as that of *M. monodi*, by its less extensive vitellaria, and by its medially situated genital pore.

Mesocoelium danforthi Hoffman, 1935
Plate II, Fig. 1

Diagnosis.—Body elongate, 1.31-1.65 long, 0.54-0.58 wide; cuticle aspinous; oral sucker 0.296-0.3 by 0.328-0.336, acetabulum 0.148-0.172 in diameter; prepharynx present but indistinct, pharynx 0.11 by 0.085, esophagus extremely short, absent in some; intestinal ceca reaching past middle of body; testes, 0.104-0.108 by 0.072-0.076, obliquely lateral to acetabulum; cirrus pouch averaging 0.146 long; ovary subspherical, 0.1-0.136 by 0.08-0.096, larger than testes, behind and sometimes contiguous with right testis; vitelline follicles comparatively sparse, from level of oral sucker to below cecal tips; excretory vesicle Y-shape. Eggs small and numerous, 0.032-0.036 by 0.019-0.02.

Type host.—*Celestrus pleii.*

Type locality.—El Yungue, Puerto Rico.

Type specimen.—USNM Helminth Coll. No. *39570.*

The type specimen was studied. *Mesocoelium danforthi* most closely resembles *M. crossophorum* but can be distinguished from the latter by the absence of refractile spicules along the margins of its oral sucker, by the position of its genital pore which is medial instead of lateral as in *M. crossophorum.*

Mesocoelium geoemydae Ozaki, 1935
Plate V, Fig. 3

Diagnosis.—Body elongate, wider anteriorly than posteriorly, 1.55-1.85 long, 0.54-0.55 wide; cuticle spinous; oral sucker 0.22-0.25 in diameter, acetabulum 0.1-0.12 in diameter; prepharynx short, pharynx 0.08 in diameter; length

of esophagus slightly more than 1.5 times the diameter of acetabulum; intestinal ceca reaching middle of body; testes, 0.14-0.2 in greatest diameter, irregularly shaped, posterior to acetabulum; cirrus pouch 0.15 by 0.07; ovary oval, 0.08-0.13 in diameter; vitelline follicles lateral, extending from midlength of esophagus to ends of ceca; excretory vesicle Y-shape, the cornual bifurcation at level of cecal ends. Eggs 0.045-0.048 by 0.027-0.03.

Type host.—*Geoemyda spengleri.*

Type locality.—Loochoo Island, Japan.

Type specimen.—Unknown.

Mesocoelium geoemydae most closely resembles *M. oligoon* and *M. incognitum,* however, it can be separated from the former by its equal-lengthed intestinal ceca since the ceca of *M. oligoon* are not of equal length; and from the latter by the characteristics mentioned earlier in the consideration of *M. incognitum.*

Ozaki (1935) reported the flame-cell pattern of *M. geoemydae* to be 2 [(3+3+3)+(3+3+3)] which is identical with that described in *M. sociale* by Sewell (1920), in *Brachycoelium trituri* by Byrd (1937), in *Margeana californiensis* by Cort (1919), and in *Glypthelmins rugocaudata* by Yahata (1934). This information adds further evidence to the author's contention that the genus *Mesocoelium* is closely related to *Brachycoelium, Margeana* and *Glypthelmins.*

Mesocoelium leiperi Bhalerao, 1936
Plate II, Fig. 2

Diagnosis.—Body elongate, 1.97 long, 0.825 wide; cuticle spinous; oral sucker 0.24 by 0.225, acetabulum 0.18 in diameter; no prepharynx, pharynx 0.065 in diameter, esophagus extremely short, 0.03 long; intestinal ceca reaching posterior boundary of middle one-third of body; testes oval, 0.113-0.123 in greatest diameter, on each side of acetabulum and partially overlapping it; cirrus sac 0.095 by 0.035; genital pore on midline, posterior to cecal bifurcation; ovary subspherical, 0.13 in greatest diameter, posterior to right testis, partially overlapping acetabulum; vitellaria of singular follicles, lateral, from level of anterior oral sucker to ends of intestinal ceca; excretory vesicle I-shape (?). Eggs 0.038-0.04 by 0.025-0.027.

Type host.—*Tropidonotus* (= *Natrix*) *piscator.*

Type locality.—Rangoon, Burma.

Type specimen.—Unknown.

Zerecero (1950) reported *Mesocoelium leiperi* in *Eumeces* sp. from Cuicatlan, Oaxaca, Mexico. This species most closely resembles *M. microon* and *M. schwetzi;* the body dimensions of the three species are within the same range. *M. leiperi,* however, can be distinguished from *M. microon* by its shorter esophagus, its longer intestinal ceca which extend to the posterior one-third of the body rather than to its midlength as in *M. microon,* and by its smaller cirrus sac the length of which is approximately one-half the diameter of the acetabulum, while that of *M. microon* is one and one-half times the diameter of the acetabulum. The diameters of the acetabula in both species are identical ($\pm$ 0.18 mm).

M. leiperi can be separated from *M. schwetzi* by its longer intes-

tinal ceca and the absence of the typical large flask-shaped cirrus sac as found in *M. schwetzi.*

Mesocoelium minutum Park, 1939
Plate IV, Fig. 2

Diagnosis.—Body oval, 0.554-1.159 long, 0.26-0.398 wide; cuticle spinous; oral sucker 0.125-0.185 by 0.095-0.182, acetabulum 0.087-0.126 by 0.09-0.12; prepharynx present, pharynx 0.042-0.076 by 0.05-0.073, esophagus 0.042-0.095 long; intestinal ceca terminate posterior to ovary near midlength of body; testes oval, partially anterior to acetabulum, 0.07-0.168 by 0.07-0.162; length of cirrus pouch approximately three-fourths the diameter of acetabulum; genital pore medial, immediately posterior to cecal bifurcation; ovary, 0.064-0.154 by 0.07-0.145, posterior to right testis and below level of acetabulum; vitellaria of compact individual follicles, lateral to and along lengths of ceca; excretory vesicle Y-shape with cornual bifurcation below ends of ceca. Eggs 0.042-0.062 by 0.019-0.034.

Type host.—***Bufo vulgaris japonicus.***

Type locality.—Niwagun, Aichiken, Japan.

Type specimen.—Helminth. Coll., Keizyo (Imperial) University, Keizyo, Tyosen, Japan.

Three specimens from Japan were examined. *Mesocoelium minutum* is most similar to *M. japonicum,* but can be distinguished from the latter by the characteristics given previously in the consideration of *M. japonicum.*

Mesocoelium travassosi Pereira and Cuocolo, 1940
Plate II, Fig. 3

Diagnosis.—Body oval, 2.67-3.11 long, 1.25-1.36 wide; cuticle spinous in anterior half of body; oral sucker 0.3-0.32 in diameter; acetabulum in anterior one-third of body, diameter of 0.2-0.24; prepharynx absent, pharynx present, inconspicuous esophagus if any; intestinal ceca extending posterior to midlength of body; ovary, 0.25-0.29 by 0.21-0.26, posterior to right testis; testes irregularly shaped, 0.25-0.3 by 0.18-0.23, situated on each side of acetabulum; cirrus pouch, 0.2 by 0.1-0.12; genital pore at point of cecal bifurcation; male and female gonads in anterior one-third of body; vitellaria of large irregularly shaped follicles, lateral to ceca, from lateral boundaries of oral sucker to near ends of ceca; excretory vesicle Y-shape (?). Eggs 0.033-0.037 by 0.025-0.026.

Type host.—***Bufo*** sp.

Type locality.—Paraiba, Brazil.

Type specimen.—Not recorded.

Two specimens from San Paulo, Brazil, were studied. *Mesocoelium travassosi* most closely resembles the generotype, *M. sociale,* however, it can be distinguished from the latter by its shorter intestinal ceca which only extend to the middle of the body while the ceca of *M. sociale* extend to the posterior one-third of the body; furthermore, the vitelline follicles of *M. travassosi* are extremely irregular in outline and are less extensive than those found in *M. sociale.*

Mesocoelium crossophorum Pérez, 1942
Plate II, Fig. 5

Diagnosis.—Body oval, 1-1.1 long, 0.4-0.5 wide; cuticle completely spinous; oral sucker 0.6-0.175 in diameter with prolonged digit-like cuticular projections along anterior and lateral margins (10-12 anteriorly, 6 along each lateral margin); acetabulum 0.13 in diameter; prepharynx present, pharynx 0.065 in diameter, esophagus extremely short; intestinal ceca reaching slightly posterior to ovary; testes oval, averaging 0.11 by 0.08, on each side of acetabulum; cirrus pouch large, length approximates greatest diameter of testes; genital pore to right of midline, lateral to esophagus; ovary rounded, 0.115 in diameter; vitelline glands independently follicular, extending from oral sucker to beyond ends of ceca and are lateral to ceca; excretory vesicle Y-shape. Eggs 0.08 by 0.065.

Type host.—*Bufo peltacephalus.*
Type locality.—Jamaica, Cuba.
Type specimen.—Unknown.

Mesocoelium crossophorum is the sole species of the genus which possesses refractile spicules along the margins of its oral sucker. The phylogenetic significance of these projections is unknown and their presence in only this species of the Brachycoeliidae is hardly sufficient evidence to postulate that the Brachycoeliidae is closely related to the Echinostomidae. Rather, the author considers *M. crossophorum* a specialized member of the genus *Mesocoelium* characterized by the presence of the refractile spicules which are independent in origin from the spines of the echinostomes.

Mesocoelium sibynomorphi Ruiz and Leão, 1943
Plate III, Fig. 3

Diagnosis.—Body elongate, 3.7-4.7 long, 1.4-1.7 wide; cuticle aspinous; oral sucker 0.325-0.331 in diameter; acetabulum 0.282-0.339 in diameter, both suckers in anterior one-third of body; prepharynx present, pharynx with diameter of 0.127-0.141, esophagus of medium length; intestinal ceca short, barely extending beyond level of ovary, in anterior half of body; testes irregularly oval, 0.268-0.339 by 0.197-0.268, on each side of acetabulum, left one slightly more anterior; length of cirrus pouch approximates diameter of acetabulum; ovary 0.212-0.367 by 0.226-0.268, posterior to left testis, below acetabulum; vitellaria of small independently follicular masses limited to areas lateral to ceca from oral sucker to ends of ceca; excretory vesicle Y-shape, cornual bifurcation posterior to cecal tips. Eggs 0.036-0.039 by 0.022-0.026.

Type host.—*Sibynomorphus m. mikanii.*
Type locality.—Coronel Pacheca, Brazil.
Type specimen.—Not recorded.

Three specimens from San Paulo, Brazil, were studied. *Mesocoelium sibynomorphi* most closely resembles *M. brachyenteron,* however, it can be distinguished from the latter by the position of its genital pore which is on the midline, anterior to the cecal bifurcation, and not posterior to the bifurcation as is found in *M. brachyenteron;* by the position of the vitellaria which are more anterior, extending from the lateral margins of the oral sucker posteriorly to the level of the

testes and not along the lengths of the ceca beyond their tips as found in *M. brachyenteron.*

Mesocoelium mesocoelium (Cohn, 1903) n. comb.
Plate II, Fig. 4

Syns. *Haploderma mesocoelium* Cohn, 1903.
Pintnaria mesocoelium Poche, 1907.
Mesocoelium schwetzi Dollfus, 1950.

Diagnosis.—Body oval with pointed anterior and tapering posterior ends; 0.98-1.65 long, 0.325-0.66 wide; cuticle spinous in anterior half of body; oral sucker 0.183-0.248 by 0.169-0.232; acetabulum 0.127-0.161 in diameter; prepharynx not seen, pharynx 0.08-0.098, esophagus extremely short (0.01); intestinal ceca reaching posterior to midlength of body; testes with diameters which approximate that of acetabulum, on each side of acetabulum; left testis slightly more anterior; cirrus pouch flask-shaped; ovary larger than testes, posterior to right testis and touching it; vitellaria of single irregularly shaped follicles, lateral to ceca, from lateral borders of oral sucker to ends of ceca; excretory vesicle Y-shape (?). Eggs 0.034-0.037 by 0.022-0.024.

Type hosts.—*Bufo regularis, Rana mascareniensis.*

Type localities.—Stanleyville, Belgium Congo, Africa; Bukama, Belgium Congo, Africa.[4]

Mesocoelium mesocoelium is the only species of the genus which possesses a flask-shaped cirrus pouch. Morphologically it most closely resembles *M. leiperi* but can be easily distinguished from the latter by its shorter intestinal ceca which extend only to the middle of the body and not to the posterior one-third as in *M. leiperi,* and by the flask-shaped cirrus pouch.

The genus *Pintnaria* was erected by Poche (1907) to receive *Haploderma mesocoelium* Cohn, 1903, an intestinal parasite of the lizard, *Draco volans,* from Java. Poche observed that the name *Haploderma* was preoccupied and hence not available, and suggested *Pintnaria* as the new name. The similarity between *P. mesocoelium* and the members of *Mesocoelium* is so striking that Odhner (1910) suggested that the two genera might be considered identical. Cohn (1903) stated that his specimens greatly resembled the members of *Dicrocoelium* and placed it in the same group.

Cohn's (1903) description of *P. mesocoelium* is the only one in existence. Neither Poche (1907) nor subsequent authors (Hughes *et al.,* 1942) have amplified the description. Cohn was not specific in delimiting the generic characteristics and his drawings (pp. 35, 36) failed to reveal any striking difference between *Haploderma* (=*Pintnaria*) and *Mesocoelium.* Of the few generic characteristics given (p. 37) only that of the extent of the uterine coils, *i.e.,* "Uterus in the posterior half of body," differs from the condition found in the members of

[4] Dollfus (1950) reported this species from two hosts, *Bufo regularis* from Stanleyville, Belgium Congo, and *Rana mascareniensis* from Bukama, Belgium Congo, but did not specify from which host the type was obtained, hence both hosts and localities are listed.

Mesocoelium. The incomplete sketch of a worm mount *in toto* (p. 35), however, showed uterine coils which reach far into the anterior half of the body. The validity of the genus *Pintnaria* is indeed questionable.

The dimensions of the body and internal organs of *P. mesocoelium* are within the same range and almost identical with those of *Mesocoelium schwetzi*, and the arrangement of the internal organs of the two species are identical. The author agrees with Odhner (1910) that the genus *Pintnaria* should be considered a synonym of *Mesocoelium*, and using the older name, reduces *M. schwetzi* into synonymy with *M. mesocoelium*.

Mesocoelium maroccanum Dollfus, 1951
Plate II, Fig. 6

Diagnosis.—Body elongate; cuticle spinous, 2-2.28 long, 0.42-0.49 wide; oral sucker 0.19-0.22 in diameter, acetabulum 0.12-0.147 in diameter, esophagus of medium length (0.058-0.085); intestinal ceca extending beyond midlength of body; testes comparatively small, approximately one-fourth the size of acetabulum, on each side of acetabulum and partially overlapping it; cirrus pouch large, length equal to twice the diameter of acetabulum; genital pore to left of midline at level of cecal bifurcation; ovary small, same size as testes (0.08-0.09 in diameter), posterior to left testis; vitellaria of small independent follicles, lateral to ceca, from level of cecal bifurcation to beyond ends of ceca; excretory vesicle I-shape (?). Eggs 0.037-0.043 by 0.023-0.026.

Type host.—*Chaloides ocellatus*.

Type locality.—Rabat, Morocco.

Type specimen.—Not recorded

Mesocoelium maroccanum most closely resembles *M. meggitti;* both species possess a genital pore which is situated to the left of the midline of the body and lateral to the esophagus. The length of the cirrus pouch of *M. maroccanum,* however, is twice the diameter of the acetabulum, while that of *M. meggitti* is equal to the diameter of the acetabulum. Furthermore, the testes of *M. meggitti* are elongate oval with diameters approximating the diameter of the acetabulum; the testes of *M. maroccanum* are only one-fourth the diameter of the acetabulum.

Mesocoelium georgesblanci Dollfus, 1954

Diagnosis.—Body elongate, 1.3-1.91 long, 0.46-0.58 wide; cuticle spinous in anterior half of body; oral sucker 0.236-0.242 in diameter; acetabulum 0.142-0.16 by 0.087; prepharynx present, pharynx 0.073-0.078 in diameter, length of esophagus subequal to diameter of acetabulum; testes oval, 0.083-0.113 by 0.13, immediately posterior to acetabulum, partially overlapping it along posterior margin; cirrus pouch large, length approximates diameter of acetabulum; genital pore median, at point of cecal bifurcation; ovary 0.075-0.085 by 0.1, posterior to left testis; vitellaria of small irregularly shaped follicles lateral to and extending from level of cecal bifurcation to ends of ceca; excretory vesicle I-shape (?). Eggs 0.023-0.027 by 0.0275-0.041.

Type host.—*Coelopeltis monsoessulana, Ipse legi.*[5]
Type locality.—Temara, North Africa.
Type specimen.—Not recorded.

Mesocoelium georgesblanci most closely resembles *M. megaloon* but it can be distinguished from the latter by the diameter of the acetabulum which is 0.14 - 0.16 in *M. georgesblanci* and 0.065 in *M. megaloon;* by the size of the testes which are 0.082 - 0.113 by 0.13 in *M. georgesblanci* and 0.181 by 0.129 in *M. megaloon;* by the position of the testes, completely medial to the ceca in *M. georgesblanci* and overlapping the ceca in *M. megaloon;* and by the vitelline follicles, smaller and situated along the entire lengths of the ceca in *M. georgesblanci,* but only along the anterior two-thirds of the cecal length in *M. megaloon.*

Mesocoelium magrebense Dollfus, 1954
Plate V, Fig. 5

Diagnosis.—Body elongate, 2.4 long, 0.66 wide; cuticle spinous; oral sucker 0.267 in diameter; acetabulum 0.1 by 0.075, no prepharynx reported, pharynx 0.1 by 0.075, length of esophagus approximately three-fourths diameter of acetabulum; intestinal ceca reaching midlength of body; right testis, 0.125 by 0.125, on same level as acetabulum; left testis, 0.145 by 0.125, posterior to acetabulum; ovary posterior to right testis, 0.17 by 0.16; cirrus pouch approximately two-thirds the diameter of acetabulum; vitellaria of singular irregularly shaped follicles extending from level of pharynx to cecal ends; excretory vesicle Y-shape. Eggs 0.025-0.028 by 0.029-0.042.
Type host.—*Zamenis hippocrepis.*
Type locality.—Tnine, Imi N'Nlit, North Africa.
Type specimen.—Not recorded.

Dollfus (1954) described this species from only one specimen. The species most closely resembles *M. burti,* but can be distinguished from the latter by the position of its acetabulum which is slightly more posteriorly placed and not adjacent to the intestinal bifurcation as in *M. burti.* In body size, *M. magrebense* is approximately two and a half times as long as *M. burti.* The ovary of *M. magrebense* is located to the right and on the same level as the left testis while in *M. burti* the ovary is on the same side but posterior to the left testis.

Mesocoelium brachyenteron Dollfus, 1954
Plate III, Fig. 4

Diagnosis.—Body oval, 3.3-4.8 long, 1.7 wide; cuticle spinous; oral sucker 0.379-0.34 by 0.33-0.381 in diameter; acetabulum 0.3-0.35 by 0.25-0.33; prepharynx present, pharynx 0.13-0.149 in diameter, length of esophagus subequal to diameter of acetabulum; intestinal ceca not reaching midlength of body;

[5] Dollfus (1954) did not clarify from which one of the two hosts the type specimen was obtained, hence both are listed.

testes 0.29-0.3 in diameter, right one on same level as left one, and left one posterior to acetabulum; cirrus pouch approximately as long as diameter of acetabulum; genital pore at point of cecal bifurcation; vitellaria consisting of individual follicles extending from level of cecal bifurcation posteriorly beyond ends of ceca; excretory vesicle Y-shape. Eggs 0.035-0.044 by 0.021-0.028.

Type host.—*Vipera lebetina.*

Type locality.—Rabat, Morocco.

Type specimen.—Not recorded.

Mesocoelium brachyenteron most closely resembles *M. sibynomorphi,* but can be distinguished from the latter by the differences previously cited in the discussion of *M. sibynomorphi.*

DISCUSSION

Because of the great morphological similarities between the species of *Mesocoelium,* the author postulates that they are monophyletic in origin. The above revision of the genus and the annotated list of recognized species are based on the morphology of adult forms. Except for the life history of *M. lanceatum* (=*M. brevicaecum*) as reported by Ochi (1930) no other life history is known within this genus; it is suspected that further contributions in life cycle studies will reduce other species into synonymy.

The following key to the species of *Mesocoelium* has been constructed using specific characteristics which the author feels are of sufficient consistency to be of value.

KEY TO THE GENUS MESOCOELIUM

1. Testes at level of acetabulum.
  2. Intestinal ceca extending beyond midlevel of body.
    3. Genital pore median, anterior to intestinal bifurcation.
      4. Testes overlap ceca .... *sociale* (Lühe, 1901)
      4. Testes not overlapping ceca.
        5. Vitellaria of minute independent follicles .... *microon* Nicoll, 1914
        5. Vitellaria of large fused follicles .... *carli* André, 1915
    3. Genital pore median, posterior to intestinal bifurcation.
      6. Cirrus pouch length approximately one-half diameter of acetabulum .... *leiperi* Bhalerao, 1936
      6. Cirrus pouch flask-shaped, its length subequal to diameter of acetabulum .... *mesocoelium* (Cohn, 1903), n. comb.
    3. Genital pore median, at level of intestinal bifurcation.
      7. Diameters of testes subequal to that of acetabulum, left testis completely overlaps acetabulum .... *marrsi* Fernando, 1933
      7. Diameters of testes shorter than that of acetabulum, vitellaria of small singular follicles .... *danforthi* Hoffman, 1935
      7. Diameters of testes greater than that of acetabulum, vitellaria of irregular, partially fused follicles .... *travassosi* Pereira and Cuocolo, 1940
    3. Genital pore lateral to midline, anterior to intestinal bifurcation.
      8. Genital pore on left of esophagus.

9. Length of cirrus pouch subequal to diameter of acetabulum .... *meggitti* Bhalerao, 1927
9. Length of cirrus pouch approximately twice diameter of acetabulum .... *maroccanum* Dollfus, 1951
8. Genital pore on right of esophagus.
10. With refractile spicules along borders of oral sucker .... *crassophorum* Pérez, 1942
10. Without refractile spicules along borders of oral sucker .... *monodi* Dollfus, 1929
2. Intestinal ceca terminating in anterior half of body.
11. Vitellaria confluent in median line.
12. Intestinal ceca reaching level of testes .... *lanceatum* Goto and Ozaki, 1929
12. Intestinal ceca not reaching level of testes .... *elongatum* Goto and Ozaki, 1929
11. Vitellaria not confluent medially.
13. Genital pore anterior to intestinal bifurcation .... *sibynomorphi* Ruiz and Leão, 1943
13. Genital pore posterior to intestinal bifurcation .... *brachyenteron* Dollfus, 1954
1. Testes situated anterior to level of acetabulum.
14. Intestinal ceca terminating in posterior half of body.
15. Genital pore on right of midline, anterior to intestinal bifurcation .... *americanum* Harwood, 1932
15. Genital pore on midline, posterior to intestinal bifurcation .... *minutum* Park, 1939
14. Intestinal ceca terminating in anterior half of body.
16. Testes contiguous .... *japonicum* Goto and Ozaki, 1930
16. Testes not contiguous .... *ovatum* Goto and Ozaki, 1930
1. Testes situated posterior to level of acetabulum.
17. Intestinal ceca terminating in anterior half of body.
18. Ovary smaller than testes .... *geoemydae* Ozaki, 1935
18. Ovary larger than testes .... *magrebense* Dollfus, 1954
17. Intestinal ceca terminating in posterior half of body.
19. Genital pore at point of cecal bifurcation.
20. Intestinal ceca of unequal length .... *oligoon* Johnston, 1912
20. Intestinal ceca not of unequal length.
21. Length of cirrus pouch subequal to diameter of acetabulum .... *mesembrinum* Johnston, 1912
21. Length of cirrus pouch longer than diameter of acetabulum .... *georgesblanci* Dollfus, 1954
21. Length of cirrus pouch shorter than diameter of acetabulum.
22. Diameter of testes smaller than that of acetabulum .... *incognitum* Travassos, 1921
22. Diameter of testes subequal to that of acetabulum .... *burti* Fernando, 1933
19. Genital pore anterior to cecal bifurcation .... *megaloon* Johnston, 1912

It is apparent from the listing of type hosts and the other records for the species of *Mesocoelium* that the members of this genus parasitize both amphibians and reptiles in which they are found in the small intestines.

The geographic distribution of *Mesocoelium* appears to be some-

what cosmopolitan, however, most of the species have been described and reported from the Far East, Australia, and South America. No species of *Mesocoelium* have ever been reported from Europe and Dawes (1946), in his monograph of the trematodes of Great Britain and continental Europe, did not record the presence of this genus in those areas. A study of the ranges of the species has not been attempted since the information available is so inadequate.

SUMMARY

The genus *Mesocoelium* Odhner, 1911 is reviewed and 28 species are recognized as valid. The diagnostic characteristics of the valid species are considered. *M. waltoni* Pereira and Cuocolo, 1940 is considered synonymous with *M. incognitum* Travassos, 1921; and *M. brevicaecum* Ochi, 1930 and *M. pearsei* Goto and Ozaki, 1930 are both considered synonymous with *M. lanceatum* Goto and Ozaki, 1929.

Pintnaria mesocoelium Poche, 1907 is considered synonymous with *Mesocoelium schwetzi* Dollfus, 1950, however, the older name *mesocoelium* is adopted in accordance with the rules of nomenclature, hence *M. mesocoelium* (Cohn, 1903) n. comb.

A key to the species of *Mesocoelium* is given.

REFERENCES

ANDRÉ, E. 1915. *Mesocoelium* carli n. sp. Trematode parasite d'une tortue africaine. *Revue suisse de Zool.,* **23**(2):91-93.

BAYLIS, H. A. 1939. Records of some parasitic worms from the Belgium Congo. *Ann. and Mag. Nat. Hist.,* 11 ser. **3**:625-629.

BHALERAO, G. D. 1927. Three new trematodes from reptiles. *Proc. 14. Ind. Sci. Cong.,* 191.

———1936. Studies on the helminths of India. Trematoda. I. *Jour. Helminth.,* **14**:163-180.

BYRD, E. E. 1937. Observations on the trematode genus *Brachycoelium* Dujardin. *Proc. U.S. Nat. Mus.,* **84**(3010):183-199.

CHATTERJI, R. C. 1931. Helminth parasites of the snakes of India. Trematoda I. *Jour. Helminth.,* **14**(3):163-189.

———1940. Helminth parasites of the snakes of Burma I. Trematoda. *Philip Jour. Sci.,* **71**(4):381-401.

CHENG, T. C. 1958. Studies on the trematode family Dicrocoeliidae. I. The genera *Brachycoelium* (Dujardin, 1845) and *Leptophallus* Lühe, 1909. (Brachycoeliinae). *Amer. Midl. Nat.,* **59**(2):67-81.

———1959. Studies on the trematode family Brachycoeliidae. II. Revision of the genera *Glypthelmins* (Stafford, 1900) Stafford, 1905, and *Margeana* Cort, 1919; and the description of *Reynoldstrema* n. gen. (Glypthelminae n. subfam.). *Ibid.,* **61**(1):68-88.

———1960. The life history of *Brachycoelium obesum* Nicoll, 1913; with a discussion of the status of the family Brachycoeliidae. *Jour. Parasitol.,* in press.

——— AND D. V. PROVENZA 1960. Studies on the trematode family Brachycoeliidae. III. The subfamilies subordinate to the Brachycoeliidae and

the status of the genus *Cymatocarpus* Braun, 1901. *Amer. Midl. Nat.*, **63**:162-168.

COHN, L. 1903. Zur Kenntnis einiger Trematoden. *Zbl. Bakt.*, **34**:35-42.

CORT, W. W. 1919. A new distome from *Rana aurora*. *Univ. Cal. Publ. Zool.*, **19**:283-298.

DAWES, B. 1946. *The Trematoda*. Cambridge Univ. Press. 644 pp.

DOLLFUS, R. PH. 1929. Helmintha I. Trematoda et Acanthocephala (Contribution à l'étude de la faune du Cameroun. II.) *Faune Colonies Françaises*, **3**(2):73-114.

———1950. Trematodes recoltes au Congo Belge par le Professeur Paul Brien (Mai-Août 1937). *Ann. Mus. Congo Belge. Zool.*, **1**(5):1-133.

———1951. Miscellanea helminthologica Maroccana. I. Queques Trematodes, Cestodes et Acanthocephales. *Arch. Inst. Pasteur Maroc.*, **4**(3):104-229.

———1954. Miscellanea helminthologica Maroccana. XVII. Distribution, geographique des distomes du genre *Mesocoelium* avec description d'especes recoltées ay Maroc. *Ibid.*, **4**(9):636-656.

FAUST, E. C. 1932. The excretory system as a method of classification of digenetic trematodes. *Quart. Rev. Biol.*, **7**:458-468.

FERNANDO, W. 1933. Contribution to Ceylon helminthology; *Mesocoelium burti* sp. nov., *Mesocoelium marrsi* sp. nov., and *Haplorchis pearsoni* sp. nov. *Ceylon Jour. Sci., Sect. B. Zool. and Geol.*, **18**(1):9-18.

GOTO, S. AND Y. OZAKI 1929. Brief notes on new trematodes. I. *Jap. Jour. Zool.*, **2**(2):213-217.

———1930. Brief notes on new trematodes. III. *Ibid.*, **3**(1):73-82.

HARWOOD, P. D. 1932. Helminths parasitic in the amphibia and reptilia of Houston, Texas, and vicinity. *Proc. U.S. Nat. Mus.*, **81**:1-71.

HOFFMAN, W. A. 1935. *Mesocoelium danforthi* n. sp. (Dicrocoeliidae) from a lizard, *Celestrus pleii* in Puerto Rico. *Proc. Helminth. Soc. Wash.*, **2**(1):9-18.

HUGHES, R. C., J. W. HIGGINBOTHAM, AND J. W. CLARY 1941. The trematodes of reptiles. Part II. Host catalogue. *Proc. Okla. Acad. Sci.*, **21**:97-104.

———, ———, AND ———1942. The trematodes of reptiles. I. Systematic section. *Amer. Midl. Nat.*, **27**(1):109-134.

JOHNSTON, S. J. 1912. On some trematode parasites of Australian frogs. *Proc. Linn. Soc. New S. Wales.*, **37** (part 2):285-362.

JOHNSTON, T. H. 1916. A census of the endoparasites recorded as occurring in Queensland, arranged under their hosts. *Proc. Royal Soc.* Queensland, **28**(2):31-79.

LÜHE, M. 1901. Zweineue Distomen aus indischen Anuren. *Centralbl. f. Bakt.* I., **30**(4):168-177.

MEGGITT, F. S. 1927. List of cestodes collected in Rangoon during the years 1923-26. *Jour. Burma Res. Soc.*, **16**:200-210.

NICOLL, W. 1914. The trematoda parasites of North Queensland. I. *Parasitol.*, **6**:333-350.

OCHI, S. 1930. Ueber die entwickelungeschiste von "Mesocoelium brevicaecum n. sp." *Okag. Ygakk. Zasshi Jg.*, **42**(2):388-402.

ODHNER, T. 1910. *Nordostafrikanische Trematoden, grösstenteils vom weissen Nil. I. Fascioliden.* (Results of the Swedish Zoological Expedition to Egypt and the White Nile 1901 under the direction of L. A. Jagerskiöld) No. 23A. Uppsala. pp. 1-170.

———1911. Zum natürlichen System der digenen Trematoden. I. *Zool. Anz.*, **37**:181-191; II. *ibid.*, **37**:237-253; III. *ibid.*, **39**:97-117; IV. *ibid.*, **39**:513-531.

ONO, S. 1930. The development of *Echinostoma campi* n. sp. in South Manchuria with special reference to the second intermediate host. *Dobuts Zasshi, Tokyo*, **43**:7-16.

OZAKI, Y. 1936. Two new trematodes from tortoise *Geoemyda spengleri* (Gmelin). *Jour. Sci. Hiroshima Univ., Ser. B. Div. 1. Zool.*, **4** (art. 6):81-90.

PARK, J. T. 1939. A new amphibian trematode, *Mesocoelium minutum* sp. nov. (Dicrocoeliidae), from Japan. *Keizyo Jour. Med.*, **10**(2):46-51.

PEARSE, A. S. 1932. Parasites of Japanese salamanders. *Ecology*, **13**(2): 135-152.

PEREIRA, C. AND R. CUOCOLA 1940. Trematoides brasileires do genero "Mesocoelium Odhner." *Arq. Inst. Biol.* (San Paulo), **11**:399-412.

PÉREZ, I. 1942. Notas helmintologicas. *Rev. Univ.* Habana, **40/42**:193-223.

RANKIN, J. S., JR. 1944. A review of the trematode genus *Glypthelmins* Stafford, 1905, with an account of the life cycle of *G. quieta* (Stafford, 1900) Stafford, 1905. *Trans. Amer. Microsc. Soc.*, **63**(1):30-43.

RUIZ, J. M. AND A. T. LEÃO 1943. Notas helmintologicas V. "Mesocoelium subynomorphi" n. sp. (Trematoda: Dicrocoeliidae). *Rev. Brasil. Biol.*, **3**(2):145-148.

SEWELL, R. B. S. 1920. On *Mesocoelium sociale* (Lühe). *Rec. Indian Mus.*, **19**:81-95.

SZIDAT, L. 1932. Parasiten aus Liberia und Französisch — Guinea. II. Teil Trematoden. *Zeitschr. Wiss. Biol. Abt. F. Zeitschr. Parasitenk.*, **4**(3): 506-521.

TRAVASSOS, L. 1921. Contribuições para o conhecimento da fauna helmintologica brasileira XV. Sobre as especies brasileiras da Brachycoeliinae. *Arch. Esc. Sup. Agric. Med. Vet. Nichtheroy.*, **5**(1-2):59-67.

———1924. Contribuicões para o conhecimento dos helminthos dos batraquios do Brazil. *Sciencia Medica*, **11**:1-11.

TUBANGUI, M. A. 1931. Trematode parasites of Philippine vertebrates III. Flukes from fish and reptiles. *Philipp. Jour. Sci.*, **44**(4):417-423.

YAHATA, M. 1934. Studies on the excretory system of *Glypthelmins rugocaudata* (Yoshida). *Jour. Sci. Hiroshima Univ. Ser. B. Div. 2, Zool.*, **3**, pp. 77-86.

YAMAGUTI, S. 1936. Studies on the helminth fauna of Japan Part 14. Amphibian trematodes. *Jap. Jour. Zool.* A. **4**(4):551-576.

———1958. *Systema helminthium.* Vol. 1. *Digenetic Trematodes*, Interscience Publishers, N. Y.

ZERECERO, M. C. 1950. Sobre la presencia di un trematode del genero *Mesocoelium* Odhner, 1911, en reptiles de Cuicatlan, Oax. *An. Inst. Biol. Mexico*, **21**:119-126.

Inter- and Intrahabitat Movements of the Rough-Skinned Newt, Taricha torosa granulosa (Skilton)

RICHARD A. PIMENTEL
California State Polytechnic College, San Luis Obispo

Qualitative data obtained by direct observation is the usual basis for conclusions on various aspects of amphibian life history. The present study involves a technique whereby a temporary pond was fenced and traps were used to study the activities of various species of amphibians. This method enabled maintenance of a record of passage into and out of the pond and correlation of these travels with environmental factors. Some of these quantitative field data plus laboratory and conventional field techniques are here applied to give a more complete picture of certain non-reproductive aspects of the life history of a western North American salamander, *Taricha torosa granulosa* (Skilton). These observations are related in their reference to movements of these newts.

Although this paper is limited to life history considerations, mention of nomenclature used seems appropriate. Recent taxonomic treatments of the genus *Taricha* (Riemer, 1958; Pimentel, 1958) show differences of opinion regarding the relationship of *torosa* and *granulosa,* i.e., are they species, or subspecies of a single species? In addition, Riemer gave good reasons for assigning two previously described subspecies, *simulans* and *twittyi,* to the synonomy of *granulosa.* This seems to be the only possible conclusion from Riemer's work. Elimination of these two races removes the last major problem, distribution pattern, from my interpretation of the relationships. I believe two species of *Taricha* now exist, *T. rivularis* and *T. torosa. T. torosa* is represented by two groups of closely related subspecies, the *torosa* group with *torosa* and *sierrae,* and the *granulosa* group with *granulosa* and *mazamae.*

The general patterns of the life histories of the two species of western North American *Taricha* are known (Chandler, 1918; Miller and Robbins, 1954; Riemer, 1958; Ritter, 1897; Smith, 1941; Stebbins, 1951; Storer, 1925; and Twitty, 1942). *Taricha* behavior does not differ greatly from that of other newts of the family Salamandridae. Part of the year is spent on land and the remainder in water. Land existence is assumed to be a time of subterranean quiescence. Aquatic life is associated with reproductive activity and larval growth. Eggs are laid in water and hatch into aquatic larval stages. The larvae metamorphose and become terrestrial. These immature animals remain on land until they attain sexual maturity. At the next breeding period, the new, as well as old, adults move to water. After adults complete reproduction they again assume an underground life. A

frequently mentioned condition in newt life history is the marked morphological difference between land and aquatic males. Most of the differences are associated with either the presence of skin turgidity in aquatic males, or its absence in terrestrial males. In *Taricha* males the turgid appearance is allied with marked reduction in dorsal coloration, smooth rather than rugose skin, and increased tail length and tail fin height.

. Only a few of the present topics have received critical attention in the past. Many individuals have described the aquatic habitat of *Taricha,* but only the already cited works of Riemer, Stebbins and Twitty give comparative treatment of the western North American newts. *T. rivularis* is a mountain brook form. In *T. torosa,* the *torosa* group inhabit both rapid moving and quiet water, but the *granulosa* group are mostly quiet water forms. It is also known that these newts display mass migrations to breeding ponds, but such movements are limited to females.

This study of *granulosa* outlines the kinds of aquatic habitats used and preferred, duration of aquatic existence, mechanisms involved in leaving and reaching ponds, sexual differences in the pattern of migration to ponds, differences in travel to temporary and permanent ponds, wanderings of aquatic newts, activity periods, sexual and habitat differences in leaving ponds, and terrestrial existence. These life history data are related in that all aspects have some bearing on movements of these salamanders.

Acknowledgments.—I am indebted to a number of individuals for assistance during this investigation. For pertinent suggestions relative to the gonadal cycle and for the use of prepared microscopic slides showing seasonal variation in *granulosa* gonads, the writer is grateful to Dr. Ernst J. Dornfeld, Oregon State College. Special thanks are due Dr. Philip C. Dumas, College of Idaho, for making observations at Oak Creek pond when neither the author nor Dr. Robert M. Storm could accumulate data. I am indebted to Dr. Robert M. Storm, Oregon State College, for his help, advice, criticism and encouragement throughout the course of study and to Dr. Glenn A. Noble, Calif. State Polytechnic College, for reading the manuscript.

PROCEDURES AND RESULTS

Methods, although varied, were simple. Direct field observations were used in all phases of this study and extended from August, 1949, through June, 1952. These observations were made in western Oregon and northwestern California, but were concentrated in the vicinity of Corvallis, Benton Co., Oregon. Both permanent and temporary aquatic habitats were explored. The most frequently observed permanent pond was Peavy Arboretum pond, 7 miles north of Corvallis. This large, man-made body of water covered approximately 3 acres and had a maximum depth of about 25 feet. More observations were made here rather than in other permanent ponds because of the proximity of the pond to our laboratories and the large numbers of newts which

could be seen readily. The temporary pond most frequented for qualitative field observations was on a shelf of Coffin Butte, an area that also contained a permanent pond. Coffin Butte is about 15 miles north of Corvallis. The Butte pond was also used because of accessibility and number of newts visible.

Experiments were conducted in both the laboratory and the field to investigate the mechanisms of homing behavior to and from ponds and the characteristics of terrestrial life. A minimum of ten trials were used in all studies.

A fenced pond facilitated the gathering of quantitative data on movements in the field, gave insight into causes of these activities, and verified laboratory experiments. This temporary pond occurred next to Oak Creek on Oregon State College property.

OAK CREEK POND

The writer participated in the Oak Creek pond study during the first two aquatic periods, 1950-51 and 1951-52. In the 1950-51 season quantitative records were started after some newts were observed in the pond. Although construction began prior to winter rains, a fence was not completed until January 8, 1951, and the traps were first checked on January 9. Both sexes were observed in the pond prior to fencing. The first male was seen on December 9, and the first female, on December 29, 1950 In the 1951-52 season the fence was secure before the first newt migrated into the pond.

Details of project construction, etc., are given elsewhere (Storm and Pimentel, 1954). It seems sufficient here to state that the fence was made of 1/4-inch hardware cloth and was ten inches high. Also, the 14x6x5 inches traps were formed of bronze window screen. Screen funnels at each end of the traps allowed newts to enter but appeared to prevent their exit. In the present paper the study area is described in some detail for the first time, and *Taricha* data are summarized and correlated with environmental factors. Also, observation methods and difficulties, as they apply to the rough-skinned newt, are treated here with greater emphasis than in the general paper.

Description of Area.—The pond, located in a pasture, is surrounded by herbacious vegetation which is kept close-cropped by cattle. The pond and fence were protected from the cattle by a barbed-wire fence (not shown on any figure). The word *fence* as used below refers to the amphibian barrier and not the barbed-wire structure. Areas labeled as vegetation consist mostly of willows (*Salix* sp.) and black cottonwoods (*Populus trichocarpa*). The location of the temporary stream entering the pond, its direction of flow, and the exiting stream into Oak Creek are diagramed (Fig. 1). Similar features are shown for Oak Creek.

The pond had a surface area, when full, of approximately one-seventh acre. The water depth varied with the rate of flow of the

entrance stream. When the stream stopped, the depth was approximately 3.8 feet. Much greater water depths, shown as peaks in Figures 3 and 4, were the result of debris accumulating on the fence across the outlet stream and causing this fence to act as a partial dam to the flow of water.

Numbered stakes were placed around the margin of the pond at ten-foot intervals (Fig. 2). These reference points aided in pin-pointing observations and were also used to designate individual traps. The number assigned to each trap was taken from the stake closest to a direct line from the trap to the pond. The only exception to this was for the inner and outer traps between stakes 42 and 43. These traps are referred to as inside and outside No. 42.5.

The fence worked as a barrier to most organisms entering and leaving the pond. The only known exceptions were some large adult rainbow trout (*Salmo gairdnerii*) that readily jumped over the fences. The barrier caused animals approaching the pond to drift into traps. Traps were placed to indicate direction of approach of the forms entering or leaving. The precision with which individual traps indicated direction of approach was dependent upon how effective each trap was in catching newts. Effectiveness was measured by the check traps (Nos. 2, 41, 43 and 64) placed closest to the traps on the inlet and outlet of the pond (Fig. 2). It is not believed that these check traps would capture many newts unless adjacent traps were ineffective. Newts entering by a landward route would probably not contact the limited area covered by the check traps. Animals entering via the stream would be caught only if the traps placed along the stream edge did not function. Because the check traps caught very few in-

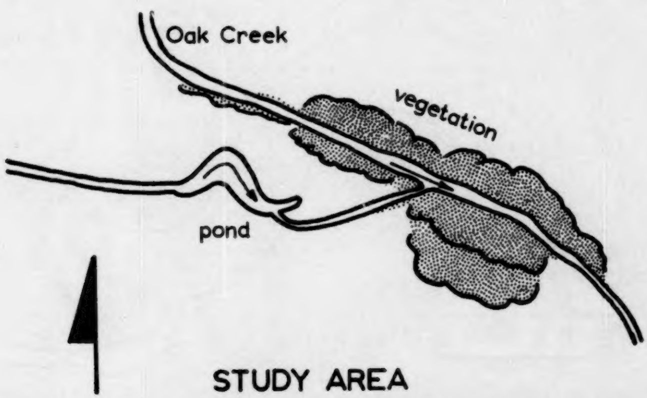


Fig. 1.—General area of study. Of special significance is the location of the study pond and vegetation along Oak Creek. Arrows indicate the direction of water flow in the study pond and in the creek.

dividuals (Figs. 5 and 6), the capture method is believed to be very effective in indicating direction of approach to the fence.

Observation Methods.—Observations were usually made daily but more frequent visits did take place. The following data were recorded for each newt: number, sex, size (if other than average), anomalies, exact point of observation, breeding condition of females (gravid or non-gravid), and degree of skin turgidity of males. In addition water level and temperature (taken at about 6" depth) were recorded. The taking of water temperatures at different levels was considered, but soon rejected, because the influx of water and shallowness of the pond led to uniform temperature throughout the depths. All of these data except size and anomalies are used in this paper.

Maximum value of observations necessitated accurate identification of individual newts. Toe-clipping was used from the start but with little hope that it would prove satisfactory. The literature at that time would have one believe that salamanders would regenerate these structures too rapidly for mutilation to be of much value. Gordon (1952) and Stebbins (1954) have since shown that this method is entirely satisfactory for certain plethodontid salamanders. For the present study toes and portions of the metacarpals were removed by deep V-shaped cuts. When animals with regenerating toes were encountered the code number was recut. This method was effective because animals marked during the first season were readily recognized the second season.

Amphibians of the study pond showed different rates and degrees

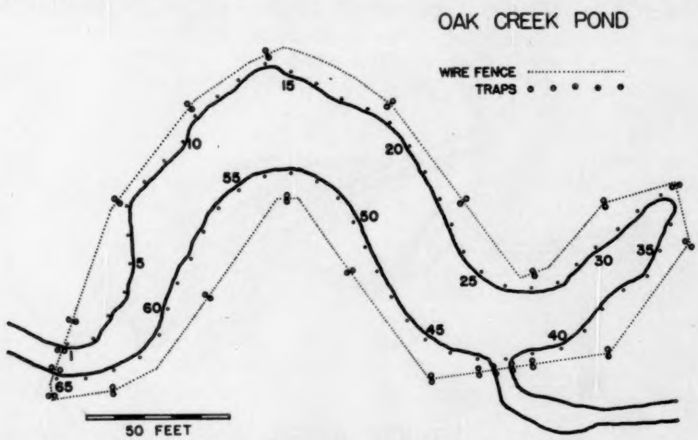


Fig. 2.—Oak Creek pond and details of project. Dotted line indicates a ten-inch high hardware cloth fence, circles indicate the position of traps, and dots indicate reference stakes placed at ten-foot intervals. Every fifth stake is numbered in the figure. Direction of water flow is from left to right.

of toe regeneration. Marking of the northern red-legged frog (*Rana a. aurora*) was most effective. Amputation in this form is believed to result in permanent loss of digits, because recaptures, including those of a year later, showed no visible regeneration. Both rough-skinned newts and Pacific tree frogs (*Hyla regilla*) were effectively numbered, but some toe replacement did occur. A gray blastema soon formed at the amputation sites in both animals. The blastema either developed into small, sometimes anomalous, lighter colored digits, or simply healed without any regeneration taking place. Toe replacement in the long-toed salamander (*Ambystoma macrodactylum*) was rapid and regenerated toes often were similar to the originals. Moreover, different toes on the same animal tended to show different rates and degrees of replacement. For this reason, it is doubtful if the recognized recaptures of the following season were assigned their proper number. It is even possible that growth could obscure markings during a single aquatic period in this ambystomid salamander. A single Pacific giant salamander (*Dicamptodon ensatus*) was trapped, but it was not recaptured.

Because of a belief that toe-clipping would prove unsatisfactory, numbered metal tags were also tried. The smallest and apparently the best of those available was a type of fingerling tag (Style 1005, Size 1,

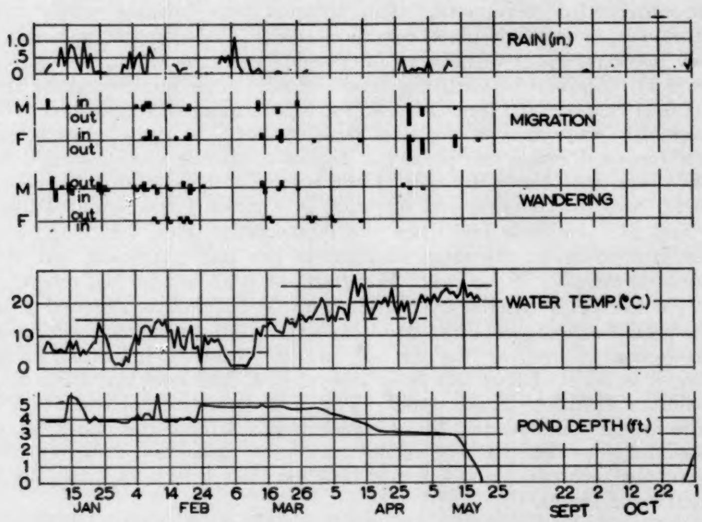


Fig. 3. Pond Data, 1950-51.—From top to bottom are graphed daily rainfall in inches; date of first entrance and final exit, males on the line above that for females; wandering, with the sexes separated as for migration; water temperature in degrees centigrade; and pond depth in feet.

National Band and Tag Co., Newport, Ky.) It was hoped that these tags could be clamped on lower jaws as was the practice with certain frogs. Laboratory newts showed immediate lower mandible ulceration around the tag. Tags placed in the fleshy portion of the base of the dorsal fin of lab newts appeared to produce no adverse reaction. However, when tags were placed on study pond newts, the fins ulcerated and the tags dropped from the tail within a few days. These tagged salamanders could always be identified later, not only by their clipped toes, but also by deformities and lighter coloration in the healed area at the base of the tail.

Difficulties.—Certain factors may have affected the data, but they are believed to have no bearing on the conclusions derived from this study. These difficulties were undermining of entrance and exit fences, the source of rainfall data, water temperature and depth, and different observers.

Breaking down of the barriers at sites of water entrance and exit occurred during periods of high water. Although it was thought that undermining could result in the loss of much data on newt movements, such was not the case. The lack of difficulty is attributed to marked reduction of newt movement at times of flood. All field observations indicate that newt activity is extremely limited on such occasions. Moreover, interpolation of data often alleviated the problem caused by unrecorded movement. Interpolation was possible when two entrances, or exits, occurred two days apart. For example, records of exit two days apart without an intervening entrance would necessitate such an entrance beneath the fence. Only three wanderings of the 1950-51 season and one of the 1951-52 season did not have the necessary prior data to pinpoint time of exit. In these cases newts last recorded inside the pond but captured outside were assumed to have been absent only one day. On this basis a "guessed time of movement" was interpolated and recorded in Figures 3 and 4 and Tables I and II. In these few cases the interpolated path, i.e., trap, was assumed to be at the same location as the last trap used, but the opposite member of the pair. For example, if an animal last recorded inside the pond entered by outside trap No. 1, it was assumed that the animal left the pond the day before via inside trap No. 1. Because no guessed movement was the only activity recorded for a particular day, it is believed that this embellishment of data does not affect the general conclusions of this paper. The purpose of interpolation of data is to give a complete picture of travel in and around the pond. It is possible, however, that entrances, wandering and exits occurred and were not recorded; but it is not believed that they took place to a significant extent.

Rainfall data were not from the area of the pond but from the Oregon State College weather station. Because the station is less than one-fourth mile from the pond and observations at both points never produced observable differences in rainfall, the data were assumed

fairly accurate. Moreover, the quantitative aspects of rainfall were not indicated to be of great significance in newt behavior. The presence or absence of ground moisture, however, is of significance. Therefore, these data from some distance are believed valid for the purposes for which they are used.

The pond was visited every day and all newt movements were recorded for the proper day. However, on certain occasions, when no newts were in traps, water temperature and sometimes water depth were not recorded. Such occasions amounted to fewer than twenty days in each season. For these days water depth is assumed and water temperature interpolated from minimum-maximum air temperatures of the weather station. This also is not believed to affect conclusions because water depth always was recorded when it was other than "near average" and weather data estimations were found to be reliable approximations of recorded water temperature. Moreover, no constant temperature recording devices were available and all temperatures, except those for maximum temperature of the second year are merely temperature of the water sometime during the day. There is an additional interpolation of environmental data; the observations from August 28, to November 17, 1951 (Figs. 3 and 4), are based on a very few recordings.

The procedures in obtaining data were of such a nature that little bias could be involved due to different observers. Storm and I usually made the daily visits together but on a few occasions only one of us checked the pond. For a short time, March 18-22, 1951, when both of us were gone, Dumas made daily records. Prior to this time Dumas became thoroughly familiar with procedures. It seems unlikely that personal bias could have resulted from the techniques of any of us.

Movements of Marked Newts.—Some confusion can result in discussion of movements because this subject is considered in different ways. First, all movements have some relationship to the time of year, i.e., a period in the annual cycle of the animal. Second, there is the type of movement itself. Finally, the mechanisms and stimuli which result in a particular movement are considered. In general, *Taricha* movements are fairly well known. From June to November, prior to the breeding season, most newts are subterranean. Upon assuming a surface existence in the latter part of the year, they spend a short time in seemingly non-oriented travel. This is referred to as either sporadic movement or the sporadic period. The brief sporadic period is terminated by breeding migration. Breeding migration is not likely to cause time of year-, type of movement-confusion because the phenomenon is well known, directional and limited to a small portion of the annual cycle. Finally, after completion of reproductive activities, postreproductive migration to underground retreats takes place. This activity is, of course, limited to a short time in an individual's annual cycle and is well known. All of these kinds and periods of movements are emphasized by the data from marked newts of the study pond.

Results.—Marking newts at Oak Creek pond disclosed a previously unreported movement made by breeding newts. During the reproductive period and prior to final exit from the pond, marked individuals were recorded leaving and then returning to the pond. In many individuals this behavior occurred many times. This movement is called wandering. The term *wandering* describes the appearance of the activity to the observer. The stimuli and behavior patterns producing the phenomenon are not known. The first movement into a pond, breeding migration, and last movement out of a pond, postreproductive migration, are not considered part of wandering.

Wandering in the above sense was displayed by twelve males and eight females in the 1950-51 season and fifteen males and ten females in the 1951-52 season. Table I indicates the more significant wanderings of individuals during the two seasons. The columns of the table denote season, i.e., 1950-51 or 1951-52; sex of the single newt involved; and movement data. The movement data include date of movement and trap of exit or entrance (abbreviated). An exit trap is designated by an asterisk; an entrance trap has no such designation. For example, an animal leaving by trap number 65 on December 31, would be recorded 12/31, No. 65*. An animal entering via trap number 65 on the same day would be recorded 12/31, No. 65. Individual wanderings are bracketed.

Much of the behavior classified as wandering at the study pond

TABLE I.—Representative wandering data

Season	Sex	Date and path of exit or entrance
1950-51	♂	(1/10, No. 65*—1/11, No. 1) (2/10, No 65*—2/11, No. 63)
	♂	(1/10, No. 65*—1/11, No. 1) (1/26, No. 65*—1/27, No. 1)
	♂	(1/24, No. 55*—1/25, No. 7) (2/4, No. 42*—2/5, No. 41)
	♀	(2/10, No. 34*—2/11, No. 34) (2/18, No. 65*—2/19, No. 1) (2/20, No. 65*—2/21, No. 1)
	♀	(2/14, No. 42*—2/15, No. 43)
	♀	(4/5, No. 65*—4/16, No. 1)
1951-52	♂	(12/21, No. 65*—12/23, No. 65) (1/12, No. 65*—1/13, No. 1) (1/27, No. 1*—1/28, No. 1) (2/3, No. 2*—2/14, No. 14) (2/16, No. 42*—2/25, No. 42.5) (4/28, No. 27*—4/29, No. 34)
	♂	(1/31, No. 62*—3/23, No. 42.5)
	♂	(2/1, No. 14*—2/27, No. 14)
	♂	(2/1, No. 34*—2/3, No. 33) (2/24, No. 42.5*—2/25, No. 42.5) (3/3, No. 1*—3/7, No. 63) (4/30, No. 41*—5/1, No. 42)
	♂	(4/19, No. 34*—4/20, No. 34)
	♀	(1/31, No. 44*—2/1, No. 43) (5/6, No. 18*—5/12, No. 14) (5/13, No. 14*—5/20, No. 14)
	♀	(2/3, No. 33*—2/4, No. 34) (4/8, No. 65*—4/9, No. 1)
	♀	(2/13, No. 65*—2/14, No. 1) (2/15, No. 65*—2/16, No. 1) (3/3, No. 65*—3/5, No. 1)
	♀	(5/6, No. 18*—5/20, No. 34)

* Designates exit trap.

may have been merely activity within an aquatic environment, because exits through aquatic traps followed by re-entrance by the same water route were classified as wandering. Although such movements are of some consequence, there is a great deal of true wandering (Table I).

Table II emphasizes pathways of movement during the two annual cycles. Here the number of individuals that existed and entered via each trap are totaled. Figures 3 and 4 graph, from top to bottom, amount of daily rainfall; dates of first entrance (above the line) and final exit (below the line), first for males and then for females; wandering (exit above and re-entrance below the line), first for males, then for females; water temperature; and depth of water in the pond.

TABLE II.—Summarization of movement data

	1950-51 Period								1951-52 Period							
Trap	Entrance		Wandering				Exit		Entrance		Wandering				Exit	
			Out		In						Out		In			
No.	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
1	6	2	..	..	19	3	..	..	5	3	2	1	9	4	1	..
2	..	..	..	..	..	..	..	..	..	2	1	..	..	..	..	..
7	1	..	..	..	1	..	..	..	1	3	..	..	..	..	..	..
11	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
14	..	1	..	1	..	1	4	3	..	3	3	1	3	2	12	5
18	2	..	..	..	..	..	..	2	1	6	..	3	..	1	1	2
23	..	..	..	..	..	..	..	..	2	3	..	..	..	..	4	2
27	..	..	..	..	..	..	..	..	2	5	1	..	..	..	..	3
32	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3
33	1	3	..	..	..	..	..	2	..	5	..	1	1	1	3	..
34	1	..	1	1	1	1	7	11	1	2	4	1	3	1	7	10
39	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
41	..	2	..	..	1	..	..	1	1	..	1	..	..	..	1	3
42	6	6	3	2	3	1	2	1	5	3	3	3	3	1	1	1
42.5	..	..	..	..	..	..	..	..	7	8	3	1	4	2	..	1
43	..	..	..	..	..	1	..	..	1	1	..	..	..	..	..	..
44	..	..	..	..	..	2	..	..	..	..	..	1	..	..	..	..
53	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..
59	..	..	..	..	..	..	..	..	1	1	..	..	..	..	..	..
63	..	..	..	..	1	..	..	..	..	..	1	..	..	..	..	..
64	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
65	..	..	22	5	..	..	3	1	2	4	5	3	1	2	2	..
Total	17	15	26	9	26	9	16	21	29	49	25	15	24	14	32	30
Were in?	31	20							17	8						
Stayed							29	10							14	25
Died							2	4								2
Total	47	35					47	35	46	57					46	57
Total Wanderers			12	8							15	10				

Figure 3 shows all environmental records starting on January 7, 1951. Newt data starts on January 9, and all information are continuous until May 20, 1951, when the pond dried up. After a gap of time, all environmental and animal observations are again recorded from September 22, to November 1, 1951. No salamanders were seen or trapped during this latter period.

Figure 4 data are complete from November 2, 1951, to May 20, 1952. The pond dried on May 20 in both years. Maximum water temperature recordings were added to Figure 4 for a short period of time, April 16, to May 20, 1952.

The two sets of pond recordings are considered to be roughly equivalent. Very slight variation does exist in water temperature and rainfall but not to the degree necessary to explain other seeming deviations. Less water depth fluctuation took place during the second season but this was not due to any environmental factor. Relatively stable water depth was the result of an upstream screen placed to catch floating debris before it could block the entrance fence. No data peculiarities can be attributed either to the screen or to reduced water fluctuation. Inconsistencies in wandering and migration, especially first entrance into the pond, can be attributed to incompleteness of the 1950-51 observations. The greater number of newts in 1951-52 would seem to account for any unexplained seasonal differences.

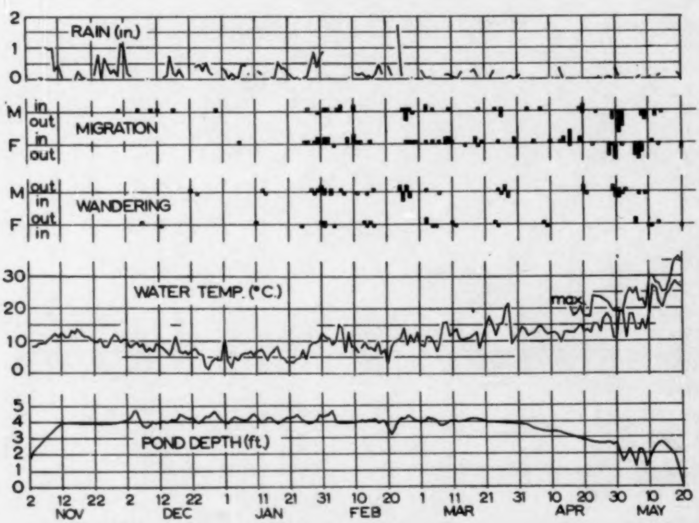


Fig. 4. Pond Data, 1951-52.—Data presented as in Figure 3. Maximum daily recorded water temperature is added for a short period in April and May.

Correlations—Various associations between newt movements and environmental factors are shown in Figures 3 and 4. Most travel occurred during periods of rainfall. Low water or air temperature are related to reduced newt activity. The lowest temperature at which movement occurred was near 5°C. High water temperature and lowering water level were associated with permanent exits from the pond. The figures indicate sexual differences in amount of activity and periods of entrance and exit.

EXPERIMENTS

In addition to study pond investigations, experiments were conducted from June, 1951, to June, 1952. The experiments were a normal outgrowth of the accumulation of data. Observations were recorded on 6x8-inch cards and filed according to a life history outline based on Fitch (1949). Reference to this file at any time showed where additional information was needed. Limited records in certain categories of the outline were the reason for various experimental studies.

Observations on the behavior of newts moving on land suggested the importance of the senses of sight and smell. Czeloth (1931) came to a similar conclusion in his work on European newts of the genus *Triturus*. Czeloth's methods were simplified and other procedures were added. Results indicate that any pond exit and entrance is accomplished by the senses. The pond data have a bearing on these laboratory results.

POSTREPRODUCTIVE MIGRATION

Pond Data.—Postreproductive migration entails movement from a pond to the autumn retreat. The concentrated areas of permanent exit indicated in Table II can be visualized by observing Figures 1, 2 and 5.

Early final departures from the study pond were aquatic. These individuals may have "lost the pond" rather than actually left as the result of innate behavior or a response to environmental conditions. This is believed to be the case because males were of the aquatic morphological phase, females were gravid, and the activity of those remaining would belie any environmental stimulus causing final exit.

Later final departures were via land traps, and are believed to be either physiological or environmental responses. The possibility of a physiological response was indicated by the newts' essentially land form. These departures occurred after the temporary stream into Oak Creek dried. They were toward, and concentrated at, the nearest dark horizon, i.e., vegetation along Oak Creek (Figs. 1 and 5).

Experimental Results.—The visual reaction to a dark horizon could be established in the laboratory. A circle, about 30 feet in circumfer-

ence and one foot high, was made of white and black paper placed on edge. This formed a ring of insignificant width and an artificial horizon about one foot high. Paper was arranged into 5 three feet wide white artificial horizons alternated with 5 three feet wide black artificial horizons. Newts believed to be making permanent exits from Peavy Arboretum pond were used for this study. Individual animals were placed under a box in the center of the ring. When the animals seemed to have quieted from previous handling the box was removed. Of 10 males and 10 females used, under ideal conditions, all repeatedly crawled toward dark (black paper) rather than light (white paper) interruptions of the horizon. The probability of either sex displaying such behavior due to chance alone is 1 in 1024. If one considers the lack of sexual difference in behavior and combines the results, the probability becomes 1 in the square of 1024. Field data also tend to establish the seeking of dark horizons as the mechanism newts use to find land habitats.

Attempts to establish the sense of smell as a factor in finding an autumn retreat were inconclusive. In the laboratory, when visual and humidity stimuli are excluded, the odor of earth causes newts to gather even if they are unable to come into direct contact with the earth. Also, under like circumstances, animals separated by a simple maze often congregate. This is believed to be an olfactory rather than a humidity response because the maze was lined with wet paper towels. In

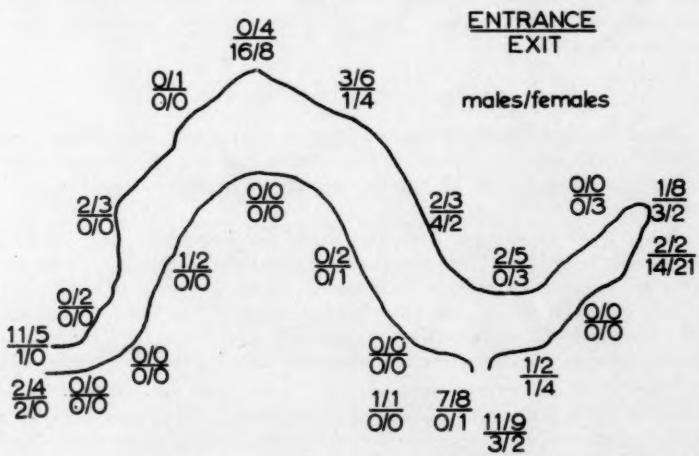


Fig. 5.—Avenues of migration to and from pond. The sexes are separated as a fraction, ♂/♀. Pondward migrations are indicated above the horizontal lines and landward migration below these lines. The data represent the total observations for both seasons. Reference to Figure 1 shows that exits are concentrated toward dark horizons, i.e., vegetation.

addition to this possible odor detection of their kind, they may perceive the odor of a given locale. The peculiar odor of a favorable hiding place seems to be a stimulus which can serve as an orientation for finding the place again. Of course this may mean that they can perceive their own odor and be seeking that rather than any particular site. These olfactory responses will either not take place or be haphazard unless favorable air currents are present. The nature of the various responses cause the belief that the sense of smell, if of importance in final departure from ponds, is secondary to vision.

BREEDING MIGRATION

Pond Data.—Breeding migrations occur overland for various distances to the breeding ponds. The pathways of entrance are indicated in Table II. Figures 1, 2 and 5 show the position of entry traps and how they relate to the surrounding terrain. During the first season of Oak Creek pond study there was a preponderance of entrances via inlet and outlet streams, and in the second season there was an even higher proportion of such entries. The difference is thought to reflect the lost data of 1950-51. In both periods most aquatic approaches were upstream, but records are insufficient to assume any significance to this fact. Land approaches into the study

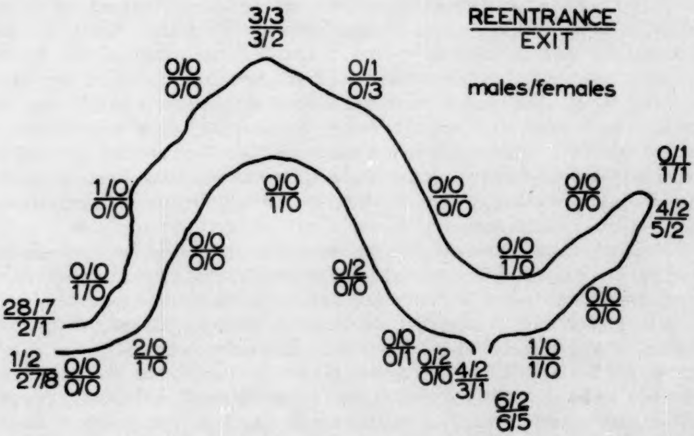


Fig. 6.—Avenues of wandering away from and back to the pond. The sexes are separated as a fraction, ♂/♀. Pathways of exit are indicated below the horizontal lines and re-entrance above these lines. The data represent the total observations for both seasons. Reference to Figures 1 and 5 show that wandering exits, like landward migrations, show concentration toward dark horizons, i.e., vegetation.

pond show some slight deviation from exit data; however, it is believed that most entrances reflect sites of subterranean life, hence indirectly direction of exit from the pond.

Stream orientation was considered as a factor in aquatic entrances. In Peavy Arboretum water flowed into the pond during periods of rainfall. This rill was along the main route of entrance. At Coffin Butte newts migrated uphill in runoff from the temporary pond. Patterns at other ponds showed some with upstream and others with downstream routes. Lack of facilities for laboratory consideration of this problem caused it to be abandoned.

Experimental Results.—Pond entrance studies were first started in the field. In these studies no association of entrance with either time of day, air or ground temperature, ground moisture, or amount of precipitation could be established. These field experiments tended to emphasize particular responses to stimuli. It was found that animals taken from the water return promptly from a distance of 3 meters. On a downhill bank the direct way to the water is immediately taken; on a level bank a preliminary wandering usually occurs before the right direction is assumed. Slightly greater delay occurs when an uphill bank is involved. Animals placed on level ground 10 meters from a pond show much variation in reactions. A few will immediately head for the pond, some will wander with seeming lack of orientation, others will seek shelter under objects and some will wander farther from the pond. Repeated field experiments displayed no sexual differences in behavior. A "typical" trial involved 25 males. Of the males released 10 meters from the pond, 7 reached the pond within fifteen minutes, 10 more within one-half hour, two more within forty-five minutes, two went under bark, and four disappeared in the underbrush away from the pond. None of these data are considered to indicate normal time responses because of the observed effects due to experimental conditions. Also, the responses may have been modified due to my presence. Such studies, however, do aid in ascertaining mechanisms of entrance.

Possible environmental aids to entrance, suggested by preliminary studies, are downhill slopes, sight, odor and humidity. Animals taken from a body of water and released on land exhibit a strong tendency to travel downhill, but migrating animals already "oriented" toward the water are geotactically indifferent. In going to ponds vision is not necessary because blindfolded newts are seemingly as successful as controls. On the other hand, if the sense of smell is blocked proper orientation seems to be due to chance, so the reaction seems to be to odor or humidity. This thought led to further laboratory work. In experiments the newts moved with odor-free currents, but toward "desirable" odor currents. When other stimuli are removed they perceive and seek areas of highest humidity. If an air current is saturated with water vapor, movement for the most part is toward the source of the current; however, travel is often with the air current.

Therefore, olfactory stimuli appear to be more significant than humidity stimuli and the animals react to air current as follows: negatively to air currents without odorous substances, positively to air currents with odorous substances and usually positively to humid air currents.

TERRESTRIAL ACTIVITY

Pond Data.—This activity is considered to include that portion of the life history between permanent exit and the sporadic period prior to breeding migration. Some members of both sexes spent subterranean life within the confines of the study pond fence. Both sexes were seen entering cracks in the dry pond bed. Added weight is given the premise of pond site underground life by the newts first seen in Oak Creek pond each season. Males were first seen on December 9, 1950, and November 1, 1951; females on December 29, 1950, and December 5, 1951. The 1951 data show the presence of newts in the pond prior to any entrances. The 1950 data probably give the same information, but this cannot be assumed because the fencing was not completed at that time.

Experimental Results.—Lack of data on terrestrial activities again resulted in laboratory studies. Use was made of a 3x8-foot enclosure in which land and water conditions could be simulated. A 2x8-foot portion became a terrarium. This was filled with earth to a depth of about one foot. The dry aquarium was screened from the land; and five males and five females, found leaving Peavy Arboretum pond, were placed into the terrarium. The newts constructed six burrows to the bottom of the enclosure. Two burrows each contained two newts and one, three newts; the rest contained individual salamanders. One burrow had a male and a female, another two males, and the other one male and two females. It is not known if salamanders sharing burrows united to construct these underground retreats. These amphibians lived almost four months underground without food or moisture in addition to that of the August subsoil they would have found near their pond. At the end of three months, although no activity was noted, a quart of water was sprinkled, as evenly as possible, over the surface of the soil. At this time none of the burrows had visible surface openings. Within 24 hours after sprinkling two males came to the surface but they returned to their underground retreats within 48 hours. It is assumed that reduced moisture, perhaps lower humidity, caused a return to subterranean existence. At the end of three and one-half months the same sprinkling process caused all males and one female to come up. Once again no open burrows were visible. Upon return of the newts underground, two days after sprinkling, water was placed in the aquarium for the first time and the barrier to the aquarium was removed. No activity was noted. Four days after the aquarium was filled, the terrarium surface was sprinkled again. The next day all males and two females were in the water. Another female entered a week later and the fourth the next day. During the time

it took the last two females to enter, the surface of the ground was kept moist. It was later found that the fifth female had died in her burrow. Males upon reaching the surface showed no visible development toward the aquatic morphology.

Sprinkling experiments and field observations indicate that rainfall stimulates subterranean newts to assume surface activity. However, rainfall was noted to stimulate all kinds of movements. At the time of the earliest fall rains only sporadic movement is stimulated. However, later in the season, rainfall may be stimulating breeding migration, wandering, or postreproductive migration as well as sporadic movement.

Allied to the above was the burial of five males and five females for a six-month period. Each was placed in a separate five quart can, the can was filled with soil to within three inches of the top and the remainder was filled with damp leaf mold. Soil and leaf mold were obtained from an area believed to contain underground retreats and were believed to have been comparable to such substrate. The cans were stored in a room where the temperature remained near 60° F. All males and three females survived. Although sluggish and visibly dehydrated when removed from the containers, they soon became active and shortly after being placed in water insufficient to cover them, the desiccated appearance was lost. The survivors showed no visible ill effects from the experiment after regaining water. These observations are the basis for the belief that the primary subterranean hazard is water loss. Finally, the conditions of this experiment are believed to be more severe than those of the usual subterranean retreat. Therefore, newts in nature probably can spend longer inactive periods without any permanent ill effects.

The above results, if accepted in their entirety, present some difficulty. In nature, individuals entering breeding ponds show morphological indication of being reproductively active; but the sexually inactive, experimental animals entered the water when they could. Perhaps this atypical behavior was due to laboratory conditions. Unfortunately no close check was kept on possible experimental animal land-water movements and no attempt was made to determine how long the animals would remain in water. Because of laboratory limitations, this project was abandoned two weeks after the first individual was known to enter the aquarium.

Because autopsies of newts removed from experimental burial showed uniform gonadal quiescence, these salamanders probably would not have reproduced that year. This agrees with the work of Miller and Robbins, (1954) on *torosa*. Their paper seems to establish an every other year breeding period for that newt. Further evidence that *granulosa* tends to reproduce every other year is indicated by the paucity of 1950-51 newts returning to the study pond in the 1951-52 season. If this cycle exists and laboratory results are dependable, individuals not breeding in a given season come to the surface and form part of the sporatic period population. At least part of this

population is in an interim stage between underground and aquatic existences. The non-reproductive animals can be distinguished from the prereproductives by gonadal condition. The non-reproductives show gonadal quiescence and prereproductives considerable gonadal development.

DISCUSSION

Movements are of four types, sporadic, pond entrance, wandering and pond exit; and take place at various times in the reproductive cycle. Upon leaving their underground retreats, newts first exhibit a kind of sporadic, seemingly non-directional activity. This is terminated by a second type, directional migration to water. Next, and also appearing to be without orientation, is wandering, i.e., exit from and return to the breeding habitat. Although wandering is characterized by a sexual difference, the significance and cause of this phenomenon are not completely clear. The last kind of travel, final exit for the season, is directional and, like most of the above behavior patterns, can be related as to cause and effect.

These four types of behavior could be diagnosed in the field only at the study pond. Here it was demonstrated that morphology is an indication, however a poor one, of the different activities. Miller and Robbins (1954), using gonadal histology and field work, diagnosed all movements but wandering and established morphological correlations with these instinctive patterns. Observations on *granulosa* adults in Oak Creek pond resulted in finding the same morphological clues to activity as those found in *torosa.* Breeding characters in sporadic movers show slight to moderate development and in pondward migrators moderate to maximum development. Wanderers display the same range of aquatic form as migrators; however, wanderers generally appear more aquatic. Exiting newts tend to exhibit the land phase. Morphologicaly, the latter are similar to sporadic movers; but landward migration is almost always later in the year, shorter in duration, and directionally away from the aquatic habitat.

The sporatic period is primarily a time of limited and secretive action. Miller and Robbins (1954) believe *torosa* takes 6-8 weeks to complete this activity. *T.t. granulosa* also wanders on land prior to migration to a pond but direct evidence for its duration is limited. One male was found on land about 100 yards to the northwest of the study pond. Twenty-one days later this newt entered the pond. The animal was observed under the same board for fifteen consecutive days, it then left and six days later was taken in an entrance trap. During the three-week period, obvious increase in aquatic morphology was noted. This delay in entrance is assumed to be related to reproductive development. The 6-8 week duration of this period in *torosa* is a reasonable estimate for its length in *granulosa.*

A series of events take place during the sporatic period. Rainfall results in subterranean newts coming to the surface. They are visibly desiccated, but a short period, less than 24 hours in the laboratory, in

moist surroundings results in recovery. The transfer from a quiescent to an active life, or perhaps some environmental factor, results in development of the secondary sexual characteristics of the male and the ova in the female. During this time the salamanders are to a limited extent on the move. The travels give the appearance of aimless, non-directional periods of foraging. Marked individuals that were recovered were found within 50 feet of the site of original encounter.

Final approaches to ponds are along definite "highways" rather than at random from all directions. This is believed to be the general case despite the lack of strongly oriented land travel into Oak Creek pond (Fig. 5) The apparently haphazard land entrances are probably associated with sites of autumn retreat. On the other hand, the large number of inlet and outlet entrances establish the streams as two pathways. Elsewhere, preferred entrance routes were noted. The primary source of newts entering Peavy Arboretum pond was from the southwest. A definite path about one-fourth mile long could be traced. The highway consisted of a portion of dirt road and a short but straight section through dense Pacific coast forest. The Coffin Butte approach was uphill along a dirt road and extended for approximately 200 yards. The latter distance seems to be about average for such routes. No other migration distance was traced as far as that at Peavy Arboretum.

Pond entrance involves at least four factors, rainfall, temperature, physiology and odors. Of possible secondary importance are humidity and slope of terrain. The triggering mechanism, starting pondward movements, is rainfall. Precipitation of this kind causes some individuals to move if temperatures are not low. However, even if temperature is optimum, the triggering mechanism will not function unless the newts are "physiologically set" for movement. It is assumed that instinctive behavior patterns associated with sexual development must progress to a certain stage before migration can take place. The final important factor effecting entrance is environmental odor. This stimulus enables animals responding to other factors to locate a pond. Two additional factors, humidity and slope, may be secondary in orienting these salamanders toward water.

Newt breeding migration is characterized by a sexual difference involving numbers of individuals found together and date of the activity. Males tend to migrate singly, females often in groups; and males migrate before females. There are no records for mass male movements to water in the genus *Taricha*. The pond influx of males is gradual and starts about a month before the first females enter. Entrance is associated with rainfall. Each subsequent rain brings additional males until sometime in November or December when the first females arrive. In contrast to lack of records of many males proceeding toward breeding grounds, there are definite reports of numerous females migrating pondward. In western Oregon such female activities were observed between the second week of January (1951) and third week of February (1952). However, not all female

movement of this kind is of the group type. Before and after such aggregations there are individual and small group migrations. The observed entrances of many females were associated with permanent ponds. In the study pond, as well as in other temporary ponds, there was little indication of coordinate female entrance. This may be due partly to fewer newts inhabiting temporary ponds which would result in fewer individuals being involved even if mass migrations occur. Final entrances show no differences, they consist of individuals of both sexes.

The rough-skinned newt is found in a wide variety of aquatic habitats. Temporary and permanent ponds, as well as lakes, are frequented the most; but streams are inhabited to some extent. Botanically sterile bodies of water are shunned, but almost any other quiet water may be occupied. Apparently suitable ponds, widely isolated from surrounding vegetation, do not have these amphibians. Although strongly alkaline waters might be avoided, *granulosa* is found in bogs of relatively low pH. Observations indicate that temperature places no strict limitation on sites, but that it does limit the duration of the aquatic period.

Wanderings from and return to impounded waters is fairly common. These seemingly aimless journeys are usually limited to short distances from the pond. At Oak Creek pond in 1950-51 this activity was recorded in 12 of the 47 males and 8 of the 35 females; in 1951-52, in 15 of the 46 males and 10 of the 57 females. These data do not indicate a statistically significant difference between the sexes as to numbers involved. At Peavy Arboretum pond, males, and to a lesser extent females, could be observed to leave the water, travel about ten feet away and return. Wanderings in the vicinity of the study pond, like those around permanent ponds, were concentrated in certain areas (Fig. 6). In fact all travel into and out of the ponds tended to be along the same routes (compare Figs. 5 and 6).

Duration of absence from the study pond during wandering was usually short. Because the traps were usually checked only once each day, the trapping system could force newts to remain out of the pond as much as 24 hours. Therefore, short land excursions, as observed in permanent ponds, could not be recorded. Males showed a stronger tendency to remain out of water than did females. Of the 1950-51 males staying out more than one day, three remained outside 2 days; two, 4 days; and one each 5, 6, 7, 9, 23, 39 and 45 days. Only three 1950-51 females remained out of the pond more than one day, two, 6 days and one 11 days. In the 1951-52 males, two remained outside 2 days; three, 4 days; and one each 9, 11, 13, 14, 26 and 51 days. In 1951-52 females, two remained outside 6 days; and one each 2, 4, 7 and 14 days. Some of this period of newt absence was associated with the onset of weather conditions unfavorable for movement. However, there is no known cause for the extensive absences of the five males.

Individual records of total wandering give additional information

on the characteristics of this phenomenon (Table I). When duration of exit was short there was a definite tendency to return through or very near the trap opposite the exit trap. When the duration was longer, return was some distance from the site of the exit trap.

Temporary terrestrial excursions from water are associated with certain environmental factors. Warm rains seem to produce marked movements of this kind around ponds, but the wanderers are not readily segregated from newts making first entrance. In the study pond wandering can be associated with rainfall and temperature. Rainfall, or at least moist surroundings, appears to be the most important factor. In addition no movement of any kind was recorded when water temperatures were below 5° C. Also, no land movement took place when air temperatures were approximately 5° C. or lower. If no rainfall occurred, movements were almost entirely confined to water. Exceptions resulted when the surrounding herbaceous vegetation was moist. These environmental associations are not unique for wandering. They are also correlated with other movements.

A puzzling side issue to the subject of this paper was the correlation of certain wanderings with newt morphology. Although on the average approximately 20 percent of the diagnostic characters of a group of *granulosa* are *torosa*-like in appearance (Pimentel, 1958), at times 90 percent of the characters of salamanders wandering near a pond were *torosa*-like. At other times all, or most, newts would be "typical" *granulosa*. No reason for this morphological association is evident.

Literature on activity periods of western *Taricha* emphasizes daylight hours. The degree of activity has been interpreted by the conspicuousness of the newts. In *granulosa* this varies according to season and habitat. As the aquatic period progresses there is first an increase and then a decrease in observability. This cycle is directly associated with courtship activities. The activity of newts also shows a difference between land and water inhabitors. Terrestrial movements are generally limited to night or overcast periods. This association may be due to humidity or other factors, e.g., it was noted that warm rains stimulate such movements. There were contradictory observations on within-pond newts. Most temporary and all permanent pond field notes show no significant difference in conspicuousness of newts during given 24 hour periods, however, in the study pond, more movement was visible at night. Despite the latter contradictory evidence the general pattern was for an equality of within-pond movement throughout the various periods of any day.

The length of aquatic existence has been neglected in previous studies. Records that exist usually do not differentiate between temporary and permanent waters. Streams are not considered here, or elsewhere in this paper, because none were found with sufficient newts to make observations reliable. In temporary ponds the extent of habitation is approximately five to seven months (December 9, 1950, to May 20, 1951, and November 1, 1951, to May 20, 1952, in the

study pond); and in permanent ponds, ten months or more. In Peavy Arboretum the last observed newt was seen on September 1, 1951, and the first entering newt on November 4, 1951, so these salamanders might have been absent fewer than 64 days. It is possible that such bodies of water are populated the year around; however, not by the same individuals.

In certain areas *granulosa* may be entirely aquatic. Certain investigators (Bishop, 1943; Farner and Kezer, 1953; and Riemer, 1958) found both sexes with vestiges of gills. Riemer found this condition in *granulosa,* the others in *mazamae.* Riemer logically interprets this as a partial tendency on the part of *granulosa* toward neoteny.

Factors related to newts leaving ponds are more numerous in temporary than in permanent aquatic environments. Evacuation of temporary situations may result from either a period of high water temperature or lowering of water level (Figs 3 and 4), but there seems to be some ability for newts to withstand these stimuli until rainfall occurs. Only temperature is likely to be of influence in permanent ponds. The impression was gained that onset of terrestrial phase morphology is hurried by increasing water temperature. Newts kept at room temperature assume the terrestrial phase much faster than newts kept at lower temperatures. Keeping males out of water also hurries the onset of the land phase. The relationship between physiology and exit is not clear. Miller and Robbins (1954) found that male California newts not only remained in water but retained the aquatic phase after regression of the gonads. This is also the case in the rough-skinned newt. Yet assumption of the terrestrial phase in male *granulosa* takes place prior to permanent departure from breeding sites. Also of possible bearing is the earlier departure of females. The situation can be summarized as follows: females depart when egg deposition is completed; many males also leave early and may be reflecting the completion of part of their physiological cycle; however, other males remain longer and stay until water temperature, other environmental changes, or in the case of temporary ponds, low water drives them to the land.

Duration of aquatic life in reflecting entrance and exit shows sexual as well as habitat differences. Males start to enter ponds before females, but final entrances show no sexual or apparent habitat distinction. In Peavy Arboretum pond the first male was observed on November 4; and the first female, on December 5, 1951. Although the study pond dates for first entrance are later, if one considers the newts that spent terrestrial life in the dry bed, the sexes become active at essentially the same time as the newts at the arboretum. In the study pond the remaining entrance activity is much the same for both sexes (Figs. 3 and 4). Conditions at other temporary, as well as at permanent ponds seemed the same. First exits show only sexual difference, males tend to leave before females. Final exits tend to display no sexual difference in temporary ponds, but males stay in permanent

ponds much longer than females. In Peavy Arboretum pond the last male was seen on September 1, and the last female on July 31, 1951. In the study pond the dates for the same year are May 14, for males and May 20, for females.

Sight and resultant movement toward dark horizons were already indicated as the means of finding underground retreats. Instinctive movement toward dark areas may result in locating more available underground habitats, but this conclusion is not readily reconciled with such things as the presence of open meadow mouse (*Microtus*) burrows on the way to permanent retreats. However, the areas producing dark horizons (woods, etc.,) tend to be more buffered against environmental extremes than are open situations. This will be considered in more detail later.

There is an inconsistency in the data proving that all newts do not leave temporary pond sites when ponds dry. In 1950-51 of the 82 Oak Creek pond inhabitants only 17 of the 47 males and 15 of the 35 females entered after the area was fenced. Although additional newts probably entered prior to fencing, some are believed to have spent their previous land period within the area of the fence. It can be seen (Table I) that twenty-nine 1950-51 males stayed inside the fence at the end of the first season, but only seventeen 1951-52 males first appeared within the confines of the fence. , For females these figures are ten and eight. The explanation of this inconsistency does not involve the simple loss of records on a few individuals because none of the newts that were inside the fence at the start of the 1951-52 period bore markings from the previous year. It is believed that these second season newts are members of a population that did not breed in 1950-51. Surprisingly, the activity of non-reproductives was never recorded within the study pond. Perhaps *granulosa* non-reproductives differ from those of *torosa* by not leaving their underground retreats until they next reproduce, but laboratory studies would belie this premise. Although of interest the activity of non-reproductives must remain a side issue of this paper. Of primary consideration is the indication that *granulosa,* like *torosa,* breeds on alternate years despite the four exceptions to be given to this pattern.

Storer (1925:51) indicated the paucity of field information on terrestrial *torosa* by stating, "Were *torosus* to breed on land like the local Plethodont salamanders it would probably be much less common in collections." Terrestrial *granulosa* are as difficult to find as any land-inhabiting salamander in western Oregon. The apparent rarity of newts on land is explained by their strong tendencies toward subterranean life. The only time truly terrestrial newts are likely to be found on the surface of the ground is during fall rains. Of the newts encountered at such times some were partially buried under debris and others had soil encrustations. Whether these were sporadic period prereproductives, showing gonadal activity, or non-reproductives, showing gonadal inactivity, was not determined. However, these and

already mentioned observations indicate that most of the period out of water is spent underground.

In western Oregon underground retreats are usually within areas of coast forest. The typical substrate is within the burrowing capabilities displayed by laboratory newts. These forests have a deep layer of humus covering the earth, so the soil is likely to retain moisture longer and to exhibit less temperature changes than that in non-forested areas. Moreover, all forest factors tend to produce the maximum buffering against environmental extremes that is available in western Oregon. Therefore, behavior seems to result in newts reaching areas most likely to enable them to withstand long periods underground.

The field data on duration of land life are quantitative only in regard to temporary ponds. Four females of the 1950-51 period returned to the study pond in the 1951-52 season. Reproductive notes on these individuals indicate that all laid eggs both seasons. The durations of absence for these females were 238, 273, 275 and 283 days respectively, so they are exceptions to the general pattern of breeding only on alternate years. Most newts spend approximately 18 months on land between reproductive periods. There was no evidence to indicate that non-reproductives became aquatic on non-breeding years.

Although many attempts were made to determine the degree of activity in subterranean newts, only one group of these salamanders was found. Three males went under a large rock on Coffin Butte on May 4, 1952. Two to three weeks later the opening was sealed. On June 5, 1952, the rock was removed and the three males disclosed. Each reacted sluggishly to a stimulus, the taking of cloacal temperatures, but all were obviously in a semi-torpid state. This condition is surprising because both the cloacal and ground temperatures were 12° C. This body temperature is generally associated with normal activity and not quiescence. Although this is an isolated record it would indicate that quiescence occurs and is of an innate physiological nature.

Water loss probably is the environmental danger of most importance on land. This danger appears to be reflected in part by the physiology and ecology of these animals. Quiescence in animals is generally considered to retard dehydration as well as other physiological hazards. Also, the underground habitats are buffered against any extreme change in environmental conditions. Moreover, a dehydration hazard is consistent with the importance of rainfall in stimulating return to surface activity. In experimental burial the obvious hazard was also dehydration. Newts are known to leave ponds and go underground during periods of rainfall. If one considers the non-reproductive phase as physiologically and instinctively specialized to prevent water loss, the fact that rainfall sometimes is associated with pondward and other times landward movements causes no difficulty. The contradictory movements are related to two entirely different phases of the life history and likely different behavior patterns.

There has already been some indirect reference to distance newts travel from ponds to underground sites. Observations were insufficient to obtain quantitative estimates. However, any distance over one-fourth mile is probably exceptional. This is believed despite the fact that a male was found about one mile from any source of surface water. At Peavy Arboretum pond most newts entered the ground within an area 20-75 feet from the pond. It is believed that at least 90 percent of the newts go underground within 200 yards of most ponds.

SUMMARY

This study of *Taricha torosa granulosa* consists of portions of the life history directly reflecting movements. It considers kinds of aquatic habitats used, duration of aquatic existence, mechanisms involved in leaving and reaching ponds, sexual and habitat differences in migration to and from ponds, wandering of aquatic newts, activity periods, and terrestrial existence. Also, reasons are given for the use of present nomenclature.

Data were obtained from direct observation, simple experimentation and studies at a fenced temporary pond. The latter give data previously unobtainable. Although morphology gives clues to types of movement taking place, only trapping data completely segregate these activities.

Pond entrance is not direct from underground retreats; perhaps six to eight weeks are spent on land. Because most newts breed only every other year, non-reproductives of the season may be involved in this period of sporatic activity. Rainfall stimulates assumption of surface life. After development of reproductives is complete, rainfall associated with favorable temperature stimulates their migration to breeding ponds. Breeding sites are found by the sense of smell; humidity perception and downhill slopes to ponds may be of some aid.

Male movement to ponds starts about a month prior to that of females and is solitary. Although females show like activity, mass migrations also occur. However, female mass migration was observed only in entrances to permanent ponds. The pondward travel of both sexes shows concentrations along certain routes or "highways" at most ponds. Final entrances are individual activities in both sexes.

Although this newt is found in a wide variety of aquatic situations it is more numerous in quiet water ponds and lakes than in streams. Vegetation-free bodies of water, as well as aquatic situations without nearby vegetation, are avoided. Normally occurring temperatures and acidities probably do not exclude them from otherwise acceptable habitats.

Land wanderings from water and back to water frequently take place and are probably stimulated by warm rains. Less than half the newts are involved. When exit is for a short time, the animals tend to move and return within the immediate area of exit; but when exit is longer, they may re-enter some distance from the site of departure.

Although a like percentage of each sex takes part in wandering, males exhibiting this behavior wander more frequently than the females. Excursions of this kind are usually of short distance and duration, especially in females; but males are known to stay out 23, 26, 39, 42 and 45 days. These activities are concentrated in the area around ponds where all land movements are most frequently encountered.

Activity in a pond appears to be equal throughout any 24 hour period; however, there is a seasonal increase in activity as the breeding period progresses and decrease as this period wanes.

The length of aquatic existence shows sexual and habitat variation. In certain localities adults of both sexes bear rudimentary gills and are probably permanently aquatic. Other males are found at least ten months in permanent ponds and about seven months in temporary ponds; females, approximately eight and six months in these habitats, respectively. Although males are observed a month longer than females in permanent ponds, temporary pond newts tend to show no sexual difference in exit dates. Departing newts have almost lost the aquatic phase morphology.

Newts leaving ponds early will use an aquatic route if it is available. However, newts that must leave ponds by a land route do so by means of vision. Seeking dark horizons is the primary mechanism for finding land retreats but the sense of smell may be of some aid. Only a tentative characterization of exit is possible. Females depart when egg deposition is completed. Many males also leave early and may be reflecting the completion of part of their physiological cycle. However, other males remain longer and stay until water temperature, other environmental changes, or in the case of temporary ponds, low water drives them to land. Not all newts leave temporary pond sites. Some enter an underground existence within the limits of the dry pond bed and most of these autumn retreats are within one-fourth mile of the breeding pond.

The underground period may be as little as three or four months for permanent pond newts. Temporary pond newts may frequently have to remain subterranean for seven months. Because most newts breed only every other year fossorial existence is usually 12 months longer. These newts can burrow to a limited extent.

The habit of seeking dark horizons for autumn retreats results in newts reaching wooded or similar areas providing optimum buffering from environmental extremes. The greatest danger to newts in these retreats seems to be dehydration. The salamanders probably assume a physiological state of quiescence while underground.

REFERENCES

BISHOP, S. C. 1943. *Handbook of Salamanders.* Ithaca: Comstock Publ. Co.: xiv + 555.

CHANDLER, A. C. 1918. The western newt or water dog (*Notophthalmus torosus*) a natural enemy of mosquitoes. *Oregon Agr. Coll. Exp. Sta., Bull.,* **15**:1-24.

CZELOTH, H. 1931. Untersuchungen über die Raumorientierung von Triton. *Zeitschr. vergl. Physiol.*, **13**:74-163.

FARNER, D. S. AND J. KEZER 1953. Notes on the amphibians and reptiles of Crater Lake National Park. *Amer. Midl. Nat.*, **50**:448-462.

FITCH, H. S. 1949. Outline for ecological life history studies of reptiles. *Ecology*, **30**:520-532.

GORDON, R. E. 1952. A contribution to the life history and ecology of the plethodontid salamander *Aneides aeneus* (Cope and Packard). *Amer. Midl. Nat.*, **47**:666-701.

MILLER, M. R. AND M. E. ROBBINS 1954. The reproductive cycle in *Taricha torosa* (*Triturus torosus*). *Jour. Exp. Zool.*, **125**:415-445.

PIMENTEL, R. A. 1958. On the validity of *Taricha granulosa*. *Herpetologica*, **14**:165-168.

RIEMER, W. J. 1958. Variation and systematic relationships within the salamander genus *Taricha*. *Univ. Calif. Publ. Zool.*, **56**:301-390.

RITTER, W. E. 1897. The life history and habits of the Pacific Coast newt (*Diemyctylus torosus* Esch.). *Proc. Calif. Acad. Sci., Zool.*, **1**:73-114.

SKILTON, A. J. 1849. Description of two new reptiles from Oregon. *Amer. Jour. Sci. Arts.*, **2**:202.

SMITH, R. E. 1941. Mating behavior in *Triturus torosus* and related newts. *Copeia*, **1941**:255-262.

STEBBINS, R. C. 1951. *Amphibians of Western North America.* Berkeley: Univ. Calif. Press: xvii + 539.

———1954. Natural history of the salamanders of the plethodontid genus *Ensatina*. *Univ. Calif. Publ. Zool.*, **54**:47-124.

STORER, T. I. 1925. The amphibia of California. *Ibid.*, **27**:1-343.

STORM, R. M. AND R. A. PIMENTEL 1954. A method for studying amphibian breeding populations. *Herpetologica*, **10**:161-166.

TWITTY, V. C. 1942. The species of California *Triturus*. *Copeia*, **1942**:65-76.

Germination Studies of Aerial Bulblets of Allium vineale L. and A. canadense L.[1]

ARNOLD KROCHMAL
Western Carolina College, Cullowhee, North Carolina

This investigation was undertaken in an effort to determine under what conditions and circumstances the aerial bulblets of *Allium vineale* L. and *Allium canadense* L. would no longer be capable of germination. The problem arose because of the incidence of these bulblets, particularly *A. vineale,* as impurities in grain crops, such as wheat and barley.

The specific problem was the question of legal definition of the term "noxious weed seed" as applied to the bulblets in state and federal seed laws. These laws generally assumed *Allium* bulblets to be capable of germination under all conditions. A number of seed companies had questioned the validity of the application of the laws without exception to situations in which the companies felt the bulblets could no longer be considered viable.

Materials

The major portion of this work was devoted to *Allium vineale;* the larger size of the aerial bulblets of *Allium canadense,* and its less frequent distribution, make it less of a pest.

The material used in the work with *Allium vineale* was collected from 1943 to 1951 inclusive, from states along the Atlantic coast, and as far west as Ohio. Only a few samples of *Allium canadense* were available when the experiments began, limiting the work with these bulblets until the summer of 1951, when a number were collected in the vicinity of Ithaca, New York. Gross differences in the two species are shown in Figure 1.

A minimum of two replications of 100 bulblets each was used for each lot tested, with three or more replications in some experiments. All bulblets were stored at room temperatures unless otherwise noted.

Procedures and Results

DETERMINATION OF STANDARD TEMPERATURE AND MEDIUM

The first step was the determination of a standard temperature and germination medium which would result in the maximum possible germination. *Allium vineale* was used in the determinations.

The mean germination percentage of all lots germinated at 68°F.

---

[1] A portion of a thesis submitted for the Doctor of Philosophy degree, Cornell University, 1952, under guidance of Dr. W. C. Muenscher.

was significantly higher than those germinated at 86°F. At the higher temperature the appearance and growth rate of various fungi was more rapid than at the lower temperature. Thus, the former was used during the course of the experiments.

The selection of a germination medium was considered with possible alternatives of the paper-towelling-germinator method, or the seed-flat, greenhouse method used by Justice and Whitehead (1942).

Two sets of two replications of eight lots of bulblets were used. One set was germinated between paper towelling, the other was planted about one-half inch below the surface of a mixture of equal parts

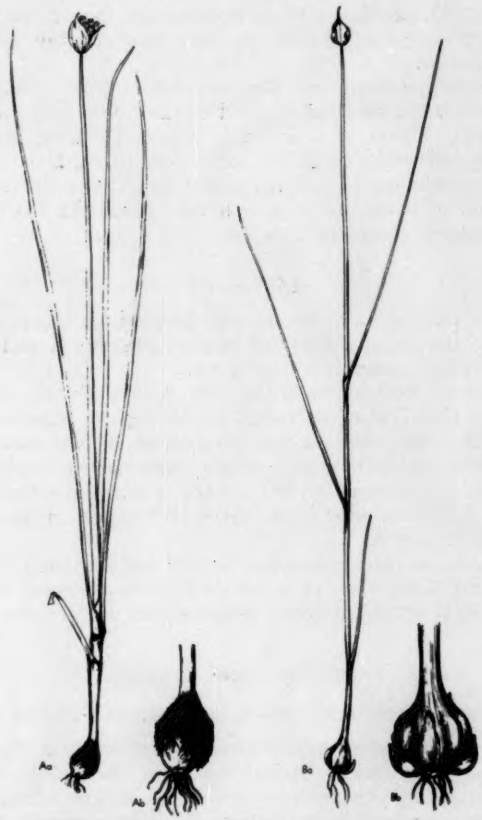


Fig. 1.—Gross distinguishing features between (A) wild onion (*Allium canadense*) and (B) wild garlic (*Allium vineale*). (Aa, Ba — habit sketches detailing origin of leaves; Ab, Bb — nature of the bulb.)

of sand, peat and soil, in seed-flats, and set in a greenhouse at a temperature of approximately 72-75°F. The results obtained at the end of a ten-day period showed only a slight decrease in the number of plants coming up in the seed-flats, as compared to the germinator methods. This fact, combined with the relative ease of running large numbers of tests in trays, as compared to seed-flats, led to the selection of the first method.

LONG-TIME STORAGE AT LOW TEMPERATURE

For the series of tests requiring long-time storage, two samples of bulblets of *Allium vineale* collected in 1951 were used. A single sample of *Allium canadense* was available. The bulblets were placed in small manila envelopes and kept in mason jars with loosely-placed glass covers, permitting air movement. The bulblets were exposed to room temperature, 72 ± 2°F. to 33°F. in an ordinary household refrigerator, and to 40°F. in a cold storage room.

Germination tests were run at about one-month intervals.

When stored at low temperatures (Table I), *Allium vineale,* harvested June 12, 1951, failed to show any germination during the trials. The bulblets held at room temperature broke dormancy in mid-November 1951, after about five months' storage. On the other hand, *Allium canadense,* harvested July 15, 1951, when held in cold storage and in the refrigerator, broke dormancy after two and one-half months. The bulblets held at room temperature broke dormancy in early January 1952, and remained consistently below the other two treatments in germination percent. The 40°F. temperature resulted in a higher germination percentage than the 33°F. temperature.

TABLE I.—The effect of prolonged storage at different temperatures on the germination of bulblets. Figures represent mean germination of two lots of 100 bulblets.

Lot[1] No.	Treatment	1951 Sep. 17	Oct. 18	Nov. 18	1952 Jan. 2	Jan. 30	Mar. 1	Mar. 28
				Allium vineale				
	72°F.±2°	0	0	9.0	17.5	23.5	20.0	15.0
1	33°F.	0	0	0	0	0	0	0
	40°F.	0	0	0	0	0	0	0
	72°F.±2°	0	0	26.5	36.5	35.5	31.0	24.0
8	33°F.	0	0	0	0	0	0	0
	40°F.	0	0	0	0	0	0	0
				Allium canadense				
	72°F.±2°	0	0	0	2	7.5	11.0	8.0
	33°F.	0	2.5	2.5	12.5	20.5	25.5	16.0
	40°F.	6	7.0	14.5	32.5	35.5	30.5	9.5

[1] All specimens were collected in the summer of 1951.

AGING AND VIABILITY

The span of viability of bulblets of these species is of interest to seedsmen who store grain and grass seed for some length of time. In order to determine how long a period would elapse before the bulblets would no longer be capable of germination, twenty-nine lots of *Allium vineale* collected from 1943 to 1950, and stored at room temperature, were tested in 1951. Fourteen lots, collected in the years 1943 through 1949, failed to germinate when tested in February; two other lots (one collected in 1948, the other 1949) had low germination percentages (see below). Similar samples of 5 lots of *Allium canadense* collected in 1945, 1948, and 1949 were tested, but none germinated.

All of the bulblets of *Allium vineale,* collected in 1950, (except Lot 79) germinated when first tested in February 1951; in April, four of the twelve 1950 samples were dead; in July, seven samples no longer were viable, and by March, 1952 only one lot was still capable of germination (Table II). This lot no longer germinated when tested in April.

One (Lot 40) of the three samples collected in 1949 germinated when first tested in February, 1951. In March it was dead. One (Lot 36) of the six samples collected in 1948 displayed weak germination (2%) when tested in February, 1951, and none after that. The bulblets collected before 1948 were dead in February, 1951; these included 3 lots in 1943, 2 lots in 1944 and 2 lots in 1945.

It is of interest to note (Table I) that maximum germination was

TABLE II.—The loss of viability of bulblets of *Allium vineale* with the lapse of time.

Lot No.	Harvest Date	1951 Feb.	Apr.	Jul.	Sep.	1952 Mar.	Apr.
		Germination percentage					
11	1950	13	1	0	0	0	0
12	1950	22	0	0	0	0	0
13	1950	38	4	3	1	0	0
15	1950	12	0	0	0	0	0
16	1950	7	0	0	0	0	0
17	1950	17	0	0	0	0	0
72	1950	42	6	0	0	0	0
73	1950	43	21	3	0	0	0
74	1950	44	9	0	0	0	0
75	1950	49	26	5	2	0	0
77	1950	42	14	4	2	0	0
78	1950	72	33	4	6	2	0
79	1950	*	*	*	*	0	0
40	1949	18	0	0	0	0	0
36	1948	2	0	0	0	0	0

* Not tested at this time.

reached within five to six months after harvest, followed by a steady decline. This is true of *A. vineale* (Table I), and is evident with *A. canadense* in cold storage.

BULBLET SHRINKAGE

Effect on Germination.—A morphological characteristic often suggested by seedsmen to distinguish between bulblets capable of germination and those not capable of growth, is size; a number of farmers and seedsmen suggest that small bulblets will not germinate.

In order to test this hypothesis, selections of bulblets were made, according to size, i.e., small, large or medium. They were then weighed and length and width were measured. The width was the measurement of the widest point on the bulblet. There was a direct relationship between size and germination (Table III). These tests were made in February 1951.

During the summer of 1951 other tests were set up with fresh material of the two species. For *Allium vineale* three lots were selected and each was arbitrarily divided into four samples, two of large and two of small bulblets; the same technique was used for *Allium canadense.* The material was stored in small manila envelopes at room temperature.

In every case except one (Lot 9) the large bulblets reached a greater maximum germination than did the small; in all cases in both species the larger bulblets maintained their viability at a higher percentage for a longer period of time (Table IV).

Although Lot 95 (Table IV) contained the smallest bulblets of any tested, it reached a higher germination percentage than any of the lots tested. The only nonviable sample at the end of the experiment was Lot 14S which contained the largest of the small bulblets used.

The bulblets of *Allium canadense* behaved in a similar manner, with the large bulblets breaking dormancy first, and reaching a higher maximum than the small bulblets.

During the germination tests, the various samples of bulblets were weighed to assay the loss of moisture, in order to determine whether there was any correlation between such loss and germination per-

TABLE III.—The relationship between size of bulblets and germination of *Allium vineale*. Each figure represents the mean for 100 bulblets.

Description	Mean weight in mgms	Mean size in cms	Mean percent germination
Small	1.63	0.39 x 0.21	10.0
Medium	3.56	0.54 x 0.23	28.0
Large	7.99	0.64 x 0.27	44.2
Random	....	....	26.5

TABLE IV.—The relationship between bulblet size and percent germination of *Allium vineale* and *Allium canadense.* Each figure represents the mean of two lots of 100 bulblets each. Harvested summer, 1951. (S = small, L = large).

Lot No.	Mean wgt. mgms. per bulblet	1951 Nov. 18	Jan. 2	1952 Jan. 30	Mar. 1	Apr. 2
			Allium vineale			
14S	10.2	0	14	0	0	0
14L	26.5	12	34	24	15	3
9S	2.1	15	78	33	35	5
9L	10.6	30	63	65	59	23
2S	7.3	12	26	30	34	12
2L	25.8	41	32	62	51	22
			Allium canadense			
S	19.7	0	9	4	2	4
L	43.2	16	25	38	55	52

centage. There was a greater average loss of moisture from the small bulblets of *Allium vineale* than from the large ones, but no appreciable difference in *Allium canadense.*

Within the *Allium vineale* series, Lot 9S reached the highest germination percentage (Table IV), and had the greatest water loss (Table V). Lot 9L exhibited the second highest rate of germination,

TABLE V.—A comparison of the moisture loss between small and large bulblets of *Allium vineale* and *Allium canadense* over a nine-month period of time. Each figure represents the mean weight (in mgms) of five hundred bulblets. Collected summer of 1951.

Lot. No. or Sample	1951 Jun. 22	Jul. 19	Sep. 7	Nov. 17	1952 Jan. 20	Mar. 27	% loss of orig. wgt.
			Allium vineale				
2S	0.732	0.680	0.645	0.584	0.521	0.452	38.29
2L	2.581	2.240	2.233	2.149	1.984	1.634	36.70
9S	0.413	0.320	0.305	0.302	0.219	0.159	61.41
9L	3.188	2.884	2.854	2.136	2.013	1.948	38.89
14S	0.203	0.134	0.122	0.111	0.092	0.085	57.97
14L	0.530	0.378	0.353	0.297	0.231	0.199	62.45
			Allium canadense				
small			2.298[2]			0.036	59.2
small			3.185			1.349	57.6
large			13.554			6.036	55.2
large			12.811			5.892	54.0

[2] Measurements taken July 28.

but had a very low rate of moisture loss. Obviously there is no relation between water loss and germination.

Bulblet Shrinkage and Re-cleaning Seed.—The idea that the outer paper covering of bulblets of *Allium vineale* remains distended while shrinkage takes place in the inner fleshy portion had been suggested in an early work (Duvel, 1907), but no data were presented to support the claim.

A group of bulblets, screened to remove the very smallest (less than 0.18 cm in diameter) and the very largest, was selected to provide the material for a test. Fifteen medium-sized bulblets with the covering intact, and fifteen with the covering removed, were used. Each individual bulblet was placed in a paper envelope, and measurements of the long axis, and the widest part of the short axis, were made at monthly intervals. The first measurement was July 16, 1951, one day after harvest. Repeated measurements were made in August, September, and October. On the last two dates there were no discernible changes.

The decrease in measurable size was negligible when bulblets with the coverings were measured, but there was a significant decrease with the naked bulblets (Table VI).

This emphasizes the fact that re-screening some time after seed harvest is a practical method of reducing the number of bulblets present in crop seeds.

CROP SEED STORED WITH BULBLETS

Crop seed, such as wheat (*Triticum aestivum L.*), crimson clover (*Trifolium incarnatum* L.), and orchard grass (*Dactylis glomerata* L.) are often stored over winter with bulblets of wild onion and wild garlic, because of the impossibility of securing complete removal. The occurrence of some injury to the crop seed from the volatile oils present in the *Allium* is a possibility. The following experiment was designed to determine whether such an effect was present.

Fifty bulblets of each species were mixed with one pound lots of clover and wheat, and stored in separate glass containers, stopped with cotton plugs, from August 1951 to March 1952. In only one instance was there any obvious effect on germination of a crop seed. The

TABLE VI.—A comparison between shrinkage of bulblets of *Allium vineale* with papery outer covering and without papery outer covering (measured in cms).

	With covering		Without covering	
	Length	Width	Length	Width
July 16	.653	.297	.549	.287
August 16	.645	.293	.495	.257
Shrinkage	0.2%	2.0%	9.8%	10.4%

presence of *Allium vineale* apparently slowed the rate of germination of wheat seed during the first 48 hours, but at the end of 96 hours there was no difference in germination of the test material as compared to the control. Two replicate lots of 100 seeds each were used.

The storage of crop seeds with bulblets of wild onion and wild garlic appears to have no harmful effects on crop seed germination.

EFFECT OF MECHANICAL INJURY ON GERMINATION

Injury by Rolling.—A number of seed houses pass seeds through rollers, particularly those with hard seed coats, such as the clovers, in an effort to crush and kill the bulblets mixed with them. A large sample of crimson clover seed (*Trifolium incarnatum*) so treated was made available by a seed house for testing. The bulblets present were very small and were tested in March and July 1951, using ten replicates of 100 bulblets each time. In no case was there any bulblet germination. The seeds had been rolled during the winter of 1950-51.

In the early spring of 1951 four samples of *Allium vineale* collected the previous summer were treated in the same scarifier, two going through once, and replicates going through twice. Those rolled once showed no marked change in germination (avg. 59%) from controls (avg. 64%), whereas those rolled twice showed a marked decrease (avg. 31%) in germination (Table VII). Apparently rolling bulblets once has little effect on germination, while rolling bulblets twice causes severe damage and results in decreased germination.

Cutting Bulblets.—Bulblets of wild garlic and wild onion showing injury to the basal end were considered as inert matter, incapable of germination.

The results of original work (Bass and Hooker, 1941; Hooker, 1942) are somewhat confusing, as in the first case, cutting bulblets resulted in failure to germinate, while the later tests by Hooker in 1942, showed that basal portions of bulblets of *Allium vineale*, as well as longitudinal portions were capable of developing.

In order to determine whether or not bulblets with either basal or apical portions missing were capable of germination, four lots of 100 bulblets of *Allium vineale* were utilized immediately after harvest in July 1951. Each bulblet in half of the sample was cut transversely. The bulblets in the other half of the sample were cut longitudinally. This treatment was repeated with a sample of *Allium canadense*. All

TABLE VII.—The effect of rolling injury on germination of bulblets. Each figure represents the mean percent germination of four lots of 100 bulblets each.

Species	Rolled once	Rolled twice	Control
A. vineale	45.0	20.0	66.0
	73.0	42.5	61.0
A. canadense	60.5	31.0	56.0

bulblet pieces of both species failed to germinate when tested in December 1951 and March 1952.

On March 28, 1952 the treatments were repeated, using bulblets from the original treated lots of both species, but the amounts of basal and apical portions left were varied. It will be noted (Table VIII) that when the lower or basal portion is missing on the bulblets of either species there is no germination (Fig. 2), but that when parts of the apical end are removed, the basal portions are fully capable of germination (Fig. 3).

There was a direct correlation between germination and the amount of basal portion left, suggesting the presence of a "meristematic" region at the base.

The very significant increase in germination obtained by cutting the bulblets in half, longitudinally, (Table VIII) can better be appreciated when it is noted that the figures representing percentage germination for the treatment are an average figure for *both* halves. Thus under Lot 7, the figure 83 percent means that a total of 166 plants were produced from 200 pieces.

The failure in germination of bulblets cut in June 1951, and tested some months later, might well be due to excess drying, the result of moisture loss from the surfaces; there also might be a question of physiological maturity. When the bulblets are collected, it is possible that there is a period of after-ripening during which foods, or perhaps auxins, move from the apical end to the basal portion of the bulblets, and that cutting before this transfer occurs, inhibits germination.

GERMINATION OF RED AND WHITE BULBLETS

The question has been frequently raised by seedmen as to the viability of white or greenish bulblets of *Allium vineale,* which they consider as being immature, and that of those bulblets exhibiting red coloring which are considered mature. One early worker (Watts, 1895) claimed to have secured 95 percent germination of immature bulblets,

TABLE VIII.—Germination of portions of bulblets cut immediately before tests, March 28, 1952 (100 bulblets cut in each test; results expressed as percent of total pieces germinating).

Portion tested	*Allium vineale* No. 2	No. 5	No. 7	No. 9	*Allium canadense*	
Upper 1/3	—	—	0	0	–	0
Upper 1/2	0	0	0	0	0	0
Upper 2/3	—	—	0	0	–	0
Lower 1/3	—	—	34	21	–	10
Lower 1/2	100	100	75	64	13	15
Lower 2/3	—	—	94	63	–	14
Longitudinal Halves	100	95	83	79	37	32
Control uncut	30	0	88	54	26	28

although he did not define his criterion of maturity. For the tests indicated below, bulblets with the papery covering intact were used as "colorless" specimens (see Fig. 1).

The red coloring matter found on some bulblets is generally at the apical, rounded portion, whereas the basal end, attached to the stem is usually lacking in this color. In unpublished work, where runing tap water was used to break dormancy, it was found that the red coloring matter is water soluble.

The data presented in Table IX show that red bulblets broke dormancy earlier and reached a significantly higher germination than did the colorless bulblets.

At the beginning of this experiment bulblets were selected for approximately equal weight (Table X). During the course of the experiment the bulblets were weighed at intervals to determine the loss of moisture. The red bulblets lost a larger percentage than did the white or green bulblets (Table X).

It is concluded that colorless bulblets are capable of germinating and must be considered as noxious weed "seeds."

BULBLET COMPOSITION

Material collected during the summer of 1951 was analyzed immediately after harvest to determine the percentages of moisture, or-

TABLE IX.—Germination percentage of red bulblets compared to white bulblets harvested in the same field on the same day (June 12, 1951). Figures are mean germination of 2 lots of 100 bulblets each.

	1951		1952		
Sample	Oct. 18	Dec. 20	Jan. 30	Mar. 1	Mar. 28
Red	1.0	16.0	24.5	26.0	26.0
White	0	0	0	1.5	1.5

Fig. 2.—Failure of development of the apical portion of bulblets (upper row, *A. canadense;* lower row, *A. vineale*). Photograph taken two weeks after cutting.

ganic matter and ash. The moisture content was determined by weighing duplicate lots of 100 bulblets after placing them in forced draft ovens for four days at 85°F. The difference between the dry weight and original fresh weight was calculated on a percentage basis. The bulblets were then ashed in a muffle furnace at 450°F. for twenty-four hours, and the final weight taken as the amount of ash. The difference between the final weight and oven dry weight was taken to be organic matter.

For *Allium vineale* the amount of water present was found to be fairly uniform, varying from a low of 55.9 percent to a high of 62.5 percent. Previous tests (Cox, 1916) have shown a far lower moisture content, with a minimum of 25.9 percent, a maximum of 41.7 percent, and an average of 37.9 percent. There was no indication given in his paper as to the elapse of time between harvest and the determinations.

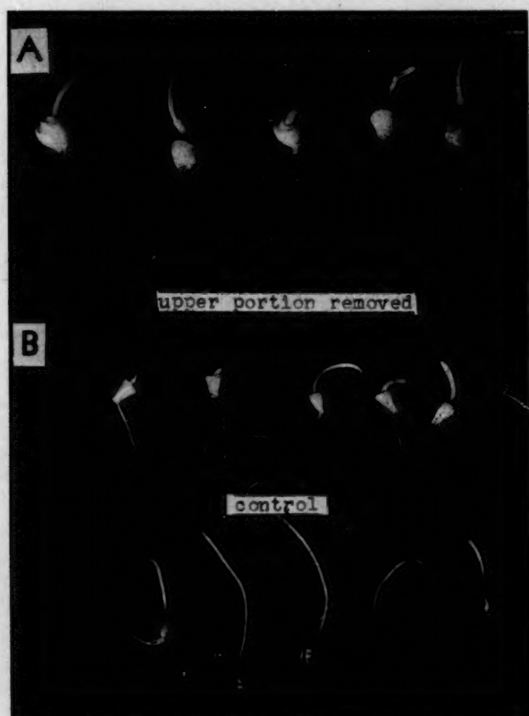


Fig. 3.—The normal development of bulblets with the apical end removed. A. — *A. canadense*. B. — Experimental and control, *A. vineale*. Photographs taken 2 weeks after cutting.

TABLE X.—A comparison of the weight loss (moisture) in mgm per bulblet between red bulblets and white bulblets of *Allium vineale* harvested in the same field on the same date, June 12, 1951. Each figure is the mean weight of 200 bulblets.

Sample	Jun. 22	Jul. 19	Sep. 7	Nov. 17	Jan. 20	Mar. 27	% of original weight
Red	1.687	1.543	1.467	1.343	1.218	1.040	61.6
White	1.857	1.848	1.691	1.646	1.527	1.364	73.4

Organic matter for *Allium vineale* varied from a low of 37.2 to a high of 43.0 percent; ash from a low of 0.3 percent to a high of 3.6. Analysis of results indicated that size of bulblets was in no way correlated with moisture content, ash or organic matter.

Bulblets of *Allium canadense* were separated into groups, according to size, and analyzed. Small and large bulblets had the same general composition.

CONCLUSIONS

Freshly harvested bulblets of *Allium vineale* placed at storage temperatures of 33°F. and 40°F. were dead after five months; bulblets of *Allium canadense* had the dormancy period shortened by storage of 33°F. and 40°F.; bulblets of both species are incapable of germination after storage at room temperature for three years.

Small bulblets of both species have a lower germination rate than do large bulblets; small bulblets of *Allium vineale* lose viability more rapidly than do large bulblets.

Shrinkage of the fleshy portion of the bulblet is considerably greater than shrinkage of the papery outer covering; serious injury decreases germination of both species; basal and longitudinal sections of bulblets of both species are capable of germination, upper portions are not; bulblets of *Allium vineale* lacking red color are capable of germination, but at a lower rate than red bulblets.

Wheat (*Triticum aestivum* L.) and crimson clover seeds (*Trifolium incarnatum* L.) are not harmed by storage with bulblets of either species.

REFERENCES

BASS, C. M. AND D. HOOKER 1941. Wild onion bulblets. *Proc. Assoc. Off. Seed Anal.*, **1941**:42-43.

COX, J. H. 1919. The drying for milling purposes of damp and garlicky wheat. *U. S. D. A. Bull.* **455** (Prof. Papers):1-10.

DUVEL, J. W. T. 1907. Garlicky wheat. *Bureau of Plant Industry Bull.* **100** (Misc. Papers III): 83 pp., 9 pls., 6 figs.

HOOKER, D. 1942. Wild onion bulblets. *Proc. Assoc. Off. Seed Anal.*, **1942**: 49:50.

JUSTICE, O. L. AND M. D. WHITEHEAD 1942. Viability of bulblets of *Allium canadense* and *Allium vineale*. *Ibid.*, **1942**:109-114.

WATTS, R. L. 1895. The wild onion (*Allium vineale*). *Tenn. Agr. Exp. Sta. Bull.*, **2**:24-34.

Book Reviews

The Viruses. Biochemical, Biological and Biophysical Properties. Volume 3. Animal Viruses. Edited by F. M. Burnet and W. M. Stanley. Academic Press, New York City. 1959. $12.00.

This is the third in a three-volume work and is the first to appear. As a general observation, the work is well-organized. Each chapter is written by an established investigator and most of the chapters are well-written. All are inclusive.

The new classification proposed is in line with recent information in virology and follows the recommendation of the various international committee meetings for nomenclature and classification held during the past few years. One small item of error which shows the rapidity of movement in the field of virology involves the inclusion of the psittocosis group as a virus. This group is now considered in the rickettsia.

The chapters on hemagglutination by S. G. Anderson and on the morphological approach by F. B. Berg present the field in a broken fashion under the classification of each group. This reviewer considers such a method stereotyped. One finds himself reading the stilted compilation, sentence by sentence, point by point, investigator by investigator, until the only way one can be sure of the point the author is trying to make is to refer back to the paragraph title, which is conveniently printed in italics.

The other chapters, 13 in all, are not quite so stilted and Chapter VI on intracellular growth by Alick Isaacs is worth the price of the book.

The bibliographic method is a poor one. It forces the reader to skip over parentheses in almost every sentence. Since this is a book, it seems to this reviewer that a small number in parentheses in lieu of the author's name and the publication date could suffice. The number would obviously refer to the bibliography for the chapter.

Further, it would be so much better if scientific writers would learn to write prose instead of an "outlinish" type of sentence and paragraph structure.

All in all the volume is a worthy effort. It is recommended as a source document but not for reading.—Thomas G. Ward, University of Notre Dame, Notre Dame, Indiana.

Utilization of Nitrogen and its Compounds by Plants. Symposia of the Society for Experimental Biology, Number 13, edited by H. K. Porter. Academic Press, Inc., New York, 1959. 385 pp., $9.50.

This volume, containing a total of 20 papers presented at the University of Reading in September of 1958, upholds the high standards of preceding symposia published by the Society and provides a broad review of various aspects of nitrogen utilization by plants. It is of interest that the included papers are by authors from Australia, England, Finland, Germany, New Zealand, Russia and the United States. The symposium as a whole underlines the need for clarifying biochemical mechanisms involved in nitrogen utilization and, further, makes apparent that an understanding of the physiological integration of such mechanisms in the living organism as a whole is only now being approached.

Possible biochemical steps and mechanisms involved in the reduction of nitrate, nitrite and other proposed intermediates in the over-all process of nitrate reduction are discussed by Nicholas in the first paper. Much of the available biochemical information in this area has been obtained from bacteria and fungi which, along with studies on algae discussed in the present symposium by

Kessler, accent the contribution which microorganisms can make to our understanding of higher plants and animals. Roberts provides an excellent discussion of the chemistry of the still-challenging process of nitrogen fixation, exploring the reasons for considering more thoroughly an oxidative first step; and Bond describes an interesting and not widely recognized group of non-legume plants which form root nodules and fix nitrogen. Amino acid formation and participation in protein synthesis in both yeast and barley, based largely on previously unpublished kinetic data collected at the University of Bristol, is described by Folkes. His remarks about alternatives to the hypothesis which considers that amino acids are formed following nitrogen uptake and then function as direct precursors of protein serve only to emphasize that today little practical validity can be attached to such alternatives. Steward describes the variety of changes which may occur in the amino acids and amides of the cell sap, and thus the physiological complexity of such changes, as environmental and nutritional conditions are varied. Present knowledge of the mechanics of amide and peptide bond synthesis — basic to mechanisms of protein synthesis — is reviewed by Webster, and the possible role of ribonucleic acid in the synthesis of protein is discussed by Heyes on the basis of studies with cultured pea roots. An unbalance in the symposium is marked by the inclusion of only a single paper concerned with the nucleic acids. Considering more specialized compounds, Mothes gives a thorough review of recent knowledge of alkaloid biosynthesis; and Fowden discusses the implications for plant physiology of a variety of newly discovered amino acids.

Though a great amount of information is summarized, wide gaps in our knowledge of nitrogen utilization become evident in the papers presented. A statement by Roberts in discussing nitrogen fixation might be considered an appropriate summary to the whole subject of the symposium. ". . . the number of proposed metabolic routes and mechanisms that are consistent with all the data is very limited; even so, none is proven, and the truth must await the gradual closing in of the attack from several different points." — EDWARD SPOERL, U. S. Army Medical Research Laboratory, Fort Knox, Kentucky.

FLORA OF ALBERTA. A manual of flowering plants, conifers, ferns and fern allies found growing without cultivation in the province of Alberta, Canada. By E. H. Moss. University of Toronto Press, Toronto, Ontario. viii + 534 pp. 1959. $10.00.

The publication of *Flora of Alberta* is a major event in North American floristic botany. Alberta, which is larger than Illinois, Indiana, Ohio, Michigan, and Wisconsin combined, is a region of great botanical interest and one that has long been in need of a comprehensive flora. It is the meeting ground of grassland and forest and of Cordilleran and boreal elements. In the extreme northeastern part of the province begins a transition from boreal to arctic. Among the floristic works usable in Alberta, the most noteworthy are Rydberg's much out-of-date "Flora of the Rocky Mountains and Adjacent Plains" (1922), including only the southern half of the province, and Budd's "Wild Plants of the Canadian Prairies" (1957), serving well in the prairie and parkland areas.

Dr. Moss's *Flora of Alberta,* the first to cover the entire province, fills admirably the need for such a work and will be indispensable for all students of the plants of Alberta and surrounding regions. The author, professor emeritus of botany at the University of Alberta, is amply qualified to write a flora of the province whose plants he has studied for some thirty-five years. In addition to the present volume, his *opus magnum,* Dr. Moss has written a series of excel-

lent articles on vegetation of the province and also a review, "The Vegetation of Alberta," which appeared in *Botanical Review* in 1955.

The main part of the Flora, following a brief and botanically uninformative preface, consist of well-constructed keys to and concise descriptions of 499 genera, 1,605 species, and 215 taxa of subspecific rank, included in 104 families of vascular plants. The more frequently encountered synonyms are listed, as are also common names when these "are known to have a considerable degree of currency." The arrangement of families is based on the Englerian system, but genera and species are arranged alphabetically to facilitate "locating genera within families and species within genera." Included are a few species not at present known in Alberta but which will "almost certainly" be found there. A glossary, a bibliography, and an index bring the book to a close.

A second edition of *Flora of Alberta* would benefit by the inclusion of more explicit distribution data — the present data are mostly so general that they are of little use to the reader who wants to know where in Alberta the various species occur. Also helpful would be the addition of brief sections on the geology, physiography, climate, vegetation, and history of floristic study of Alberta.

The book is sturdily and attractively bound and is well printed, on thin but strong paper, with an exceptionally readable type. The use of an especially prominent bold-face type for scientific names is most welcome. The *Flora of Alberta* is a highly valuable, taxonomically up-to-date, and much needed work. Dr. Moss and the University of Toronto Press deserve our heartiest thanks and congratulations for a job well done. — JOHN W. THIERET, Chicago Natural History Museum.

HANDBOOK OF GASTROPODS IN KANSAS. By A. Byron Leonard. Museum of Natural History, University of Kansas, Lawrence, Kansas. 1959. Paper bound, $1.00, cloth bound, $2.00.

This is unquestionably the best conceived state handbook on snails yet published. The presentation of complete data on local distribution, copious ecological notes, and available data on life histories make this of use to the professional malacologist. The keys, general sections, and illustrations are intended to aid the amateur collector or general naturalist. Its plan may well serve as a model for others.

Unfortunately, the execution was not equal to the design, the book showing numerous signs of carelessness or just plain sloppy work. The illustrations are from generally poor photographs which have been heavily and crudely retouched, sometimes beyond the point of recognition. The figures on plate 11, for example, are grotesque parodies of the species they are supposed to represent. The introductory line drawings (figs. 1-19) are copied from other sources (without acknowledgment) or are extremely poor originals.

More important are several major errors of omission. The transmission date of the manuscript is given as April 30, 1959. Yet the general discussion on the classes of mollusks (pp. 13-14) does not mention the zoological discovery of the decade, the segmented mollusk *Neopilina*. Described in 1957, this creature has been pictured in *Life* and *Natural History*, mentioned several times in *Science*, and even in some textbooks. Similarly, the section on the Lymnaeidae (pp. 47-56) ignores Hubendick's 1955 monograph, and the discussion of *Pomatiopsis* (p. 35) fails to cite any of the numerous studies produced at the University of Michigan from 1956 to date. In the land snails, Archer's 1947 paper on *Stenotrema* and Webb's admittedly difficult studies on slugs were not consulted.

These omissions of well-known papers are understandable if the citation on the title page acknowledging "the technical assistance of E. J. Roscoe, L. D. Fairbanks, C. D. Miles, and Tong-Yun Ho" is understood. The degree of "technical assistance" can probably be measured by comparing the text of the "Handbook's" *Succinea* section with Miles' 1958 paper (Univ. Kansas Sci. Bul., 38:1499-1543, 1 pl., 10 figs.). The Leonard "Handbook" is a word for word copy, omitting only a few tables of measurements and some discussion sections. Nowhere is this stated.

The rest of the landsnail section was written by E. J. Roscoe and the fresh-water snail section by L. D. Fairbanks and Tong-Yun Ho. It is, of course, impossible to know how much editing of these articles was done by Leonard. The large number of major errors of omission, however, would seem to argue that few changes and additions were made from the original manuscript. These errors, then, can be seen as the faults of beginning students.

It is perhaps more charitable to consider this a slipshod editorial job, than to believe that a zoologist of Dr. Leonard's position would be so unaware of developments in his own field.

The "Handbook" can be used by amateurs, although the glossary is in-adequate to enable an amateur to use the keys, and the illustrations are unusable. It does contain much new locality data and is very well-designed and printed. It is a shame that its polished appearance contains so much inaccu-rate and sloppy work.

Finally, why the pretentious title "Handbook of gastropods in Kansas"? Why not a more widely understood "Handbook of snails in Kansas"? — ALAN SOLEM, Chicago Natural History Museum, Chicago, Illinois.

DRAWINGS OF BRITISH PLANTS Part XIII. Umbelliferae (2) Araliaceae. Cornaceae. 30 Plates. By Stella Ross-Craig. G. Bell & Sons, Ltd., London. 1959. 9/6. ($1.33).

This part presents the remaining 27 species in 16 genera of Umbelliferae native to the British Isles together with *Hedera helix* and 2 species in 2 genera of Cornaceae. Of the umbellifers, at least 8 species are cultivated, adventive or naturalized in this country, including the carrot, fennel, cow- and common parsnips, and garden angelica. *Hedera helix* (English Ivy) is well-known here and has been praised and vilified by gardeners across the country and often for the same reasons concerned with its growth habits. One of the two representatives of the Cornaceae, *Thelycrania sanguinea* (*Cornus sanguinea*) is a shrub frequently cultivated.

Beautiful, perspective views and magnified sections of flowers and fruits in addition to leaves, bristles and hairs, underground parts, and general characteristics of patterns of growth are shown in these drawings. The detailed and so clearly represented views of the floral parts, particularly, will be very helpful in identification and in becoming acquainted with some aspects of the morphology of these families.—L. G. KAVALJIAN, Sacramento State College, Sacramento, California.

INSTRUCTIONS FOR AUTHORS

Manuscripts should be typewritten, double-spaced, with ample margins, on one side of 8½ x 11 inch paper. Tables and figures should be placed at the end of the manuscript. Each sheet should be numbered consecutively. The title and author's name along with the full mailing address of the author should be placed on the first page.

Style, arrangement, spelling, and abbreviations should conform to the usage of recent numbers of this journal. Do not underline any words except scientific names. Acknowledgments can be included in the Introduction, or may be offered as a footnote attached to the title of the article. Papers should be concisely written. A subsidy will be required for papers which exceed twenty journal pages in length.

References should be listed alphabetically by authors' names. In the text they should be cited by author and date, e.g., Smith (1958). The form of the citations should be that used in this journal; in references to papers in periodicals, titles should be given and inclusive page numbers are required. All citations should be checked with the original articles. Abbreviations of the names of periodicals should conform with the listings in BIOLOGICAL ABSTRACTS 29(5):v-xxxv (May, 1955), or 30(5):xi-xxxii (May, 1956). Book citations should include author's name, complete title, edition, name and location of publisher, and total number of pages.